

THE COMMUNITY STRUCTURE OF THE MIDDLE CAMBRIAN PHYLLOPOD BED (BURGESS SHALE)

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ABSTRACT. The palaeoecology and taphonomy of the Middle Cambrian Phyllopod Bed fauna (Burgess Shale, British Columbia) is described. Examination of over 30 000 slabs of shale and more than 65 000 specimens, many of them showing soft-bodied preservation, provides estimates of numbers of individuals and biovolumes of approximately 100 genera belonging to twelve major groups. Life habits are diverse with a sessile and vagrant infauna and epifauna, together with a nekto-benthos, being recognized; components of a separate pelagic community are also present. Trophic analysis documents deposit feeders, suspension feeders, predators, and scavengers, and reconstructs the trophic nucleus and a feeding web. Possible niche structure of various ecological categories is discussed in the context of dominance diversity curves. Most distributions are log-normal, but for epifaunal vagrant deposit (collector) feeders a geometrical distribution may support the hypothesis of niche pre-emption. Comparisons are drawn between the community structure of the Phyllopod Bed biota and typical Cambrian shelly faunas. In isolation the shelly component of the Phyllopod Bed has a typical Cambrian aspect, but it accounts for only *c.* 14% of genera and perhaps as little as 2% of individuals alive at the time of burial. Synecological pronouncements based on normal Cambrian assemblages are suspect, and the likely importance of predation is emphasized.

The wider implications of this study include comparisons with younger Palaeozoic deeper-water communities in an attempt to trace the evolution of ecological analogues through time. This exercise is conducted in terms of broad categories of carnivores, suspension and deposit feeders. Some groups such as sponges, ostracodes, and trilobites persist, but probably changed in relative importance. In other cases there is evidence for ecological replacement; one example could be the rise of nautiloids and eunicid polychaetes as carnivores and scavengers.

UP to 70% or more of species and individuals in a modern marine macrobiota may be effectively soft bodied (taken here to include lightly skeletized species) and possess a minimal fossilization potential (Johnson 1964; Lawrence 1968; Macdonald 1976). An upsurge in taphonomic studies has reinforced earlier conclusions that the fossil record is inevitably a seriously biased sample of original biotic diversity (e.g. Lawrence 1968; Schopf 1978; Boucot 1981; and many others). Almost all studies of fossil assemblages are restricted to a time-averaged shelly component (see Walker and Bambach 1971) that in most cases probably bears little comparison with the original living community, although attempts exist to estimate original standing crops (Stanton *et al.* 1981). Trace fossils may provide an indication of soft-part diversity, but incorporation of such data is fraught with problems. A plurality of traces may result from the varying behaviour of one species, or two or more unrelated species (even of different phyla) may make indistinguishable traces. Many animals, including soft-bodied species, may not produce preservable traces (see e.g. Hertweck 1972), while information may be duplicated when shelly species create traces. In the absence of soft-part preservation many fossil community studies are literally 'fleshed-out' with a variety of uniformitarian assumptions based on observations amongst modern faunas; the validity of such exercises has been succinctly discussed by Scott (1963).

In view of these difficulties, why have those Lagerstätten with extensive soft-part preservation not been used as a direct source of otherwise missing information? Their comparative neglect from the viewpoint of community and palaeoecological analysis (see Cisne 1973*b* and Schram 1979 for exceptions) presumably lies in their elevation to a unique status, isolated from the mainstream of study of fossil associations.

Just suppose that the extraordinary conditions of preservation in the Phyllopod Bed had failed to materialize, so that only shelly fossils remained (Conway Morris 1981). The precise composition of

this assemblage would vary according to taphonomic conditions, but in this quiet muddy environment the fauna might be expected to include trilobites, brachiopods, monoplacophorans, hyolithids, rare echinoderms, and sponges, the latter two groups mostly as scattered ossicles and spicules, respectively. This assemblage is little different in terms of major groups from many other Cambrian faunas, and as noted below many of the shelly genera have a broad geographical distribution; in the absence of soft-bodied fossils the Phyllopod Bed fauna would have no special claim for attention (see also Conway Morris and Robison 1982). Nevertheless, this is not meant to imply that the Burgess Shale is typical of *all* communities, and there is evidence for it perhaps being a conservative fauna (Conway Morris and Robison 1986). Prevailing palaeo-oceanographic conditions may also have been a factor in favouring certain faunal assemblages and promoting (or retarding) an environment conducive to soft-part preservation with cold, poorly oxygenated water providing propitious conditions.

The main purpose, therefore, of this paper is to explain how study of the Phyllopod Bed soft-bodied fauna yields palaeoecological insights into a Cambrian community that are not available from the shelly assemblage. This is because the latter accounts for little of the taxonomic diversity and a trivial percentage in terms of individuals. With regard to taxonomic composition the fauna is dominated by arthropods but, unlike the great majority of other Cambrian assemblages, trilobites are an inconspicuous component. Study of ecological categories according to position relative to substrate and feeding type, in terms of numbers of individuals and biovolumes, permits a far more extensive characterization of a Cambrian community than has hitherto been possible; the role of predators is given particular attention. Some aspects of the synecology of the Phyllopod Bed biota have been briefly reviewed elsewhere (Conway Morris 1979*b*), but that introductory analysis was both brief and based only on numbers of genera. The data for this study were collected mostly in 1979, and only a summary of the major conclusions has been published (Conway Morris 1981).

THE SETTING OF THE PHYLLOPOD BED FAUNA

Introductory remarks

The redescription of the Burgess Shale (Stephen Formation) biota was initiated by Whittington (1971*a, b*), following the reopening of the Walcott and Raymond Quarries by the Geological Survey of Canada in 1966 and 1967. Recent review papers have summarized our enhanced understanding of this biota and its place in Cambrian life (Conway Morris 1979*a, b*, 1982; Conway Morris and Whittington 1979, 1985; Whittington 1980*a*, 1981*a*, 1982). In one of these reviews Conway Morris (1979*a*) suggested that within the Phyllopod Bed, exposed only in the Walcott Quarry and the source of the great majority of specimens from the Burgess Shale, a single benthic community was recognizable. This was termed the *Marrella-Ottoia* community after the abundant epifaunal arthropod and infaunal priapulid worm respectively. In addition rare pelagic species were taken to represent the *Amiskwia-Odontogriphus* community, members of which were trapped only infrequently by the turbidity currents responsible for transporting and burying the benthic community. In the stratigraphically higher Raymond Quarry, a benthic assemblage distinct from the *Marrella-Ottoia* community of the Phyllopod Bed was identified. New discoveries of soft-bodied faunas in the vicinity of the Burgess Shale include examples from Mount Field and Mount Stephen with a marked similarity to the Raymond Quarry fauna (Collins *et al.* 1983) and lend credence to the notion that this is indeed a distinct community. Apart from scattered specimens recovered from float on Mount Field no direct counterpart to the *Marrella-Ottoia* community has yet been discovered beyond the Walcott Quarry (Collins *et al.* 1983). It is significant, however, that with few exceptions the soft-bodied taxa found in these adjacent localities also occur in the Phyllopod Bed, albeit in very varied proportions. Thus, while the Phyllopod Bed fauna was probably only one of several benthic communities (possibly intergrading) in the area, its gross faunal composition is representative of the overall faunal diversity of this basin.

Evolutionary setting

The evolutionary importance of this fauna should be considered in the context of early metazoan evolution. Whether or not metazoans first appeared far back in the Precambrian (e.g. Kauffman and Steidtmann 1981; Kauffman and Fürsich 1983; Runnegar 1982), the available fossil record points to a rapid increase in metazoan diversity, exponential at the taxonomic level of order (Sepkoski 1978), reflecting a series of adaptive radiations that originated in the Vendian. This climb in diversity levelled out during the mid-Cambrian to give an apparent 'evolutionary lull', with a limited rise in diversity over about 15 Ma (c. 540–525 Ma), prior to a further episode of major diversification during the late Cambrian and Ordovician (Sepkoski 1978, 1979, 1981*a, b*). The age of the Burgess Shale (c. 530 Ma) means that it lies within this 'lull', and so is well placed to show the relative richness of Cambrian life in terms of both ecologies and biotic diversity as an end-result of these early adaptive radiations. Cambrian shelly marine faunas had a distinct identity that stands in contrast to those of the later Palaeozoic (Sepkoski 1979, 1981*a, b*, 1984; but see Ludvigsen and Westrop 1983), and it is important to determine whether the soft-bodied component showed a comparable distinction (see below).

Regional setting

Restoration of possible Cambrian palaeo-continental configurations place British Columbia within the tropical zone at about 15° N. (Kanasewich *et al.* 1978; Scotese *et al.* 1979). A near-equatorial position for the Burgess Shale is thus significant if latitudinal diversity gradients existed, because faunas such as that in the Phyllopod Bed may have approached maximum diversity for this particular deeper-water biofacies.

Much of the Phyllopod Bed fauna appears to have been benthic, inhabiting basinal muds and silts deposited beside a precipitous algal reef that was ultimately overwhelmed by clastic deposition (McIlreath 1977; Aitken and McIlreath 1984; see also Surlyk and Hurst 1984, fig. 4 for a remarkably similar occurrence in the Silurian of North Greenland). The sheer reef (Cathedral escarpment) marks unusually sharply the boundary between the median carbonate and outer detrital sedimentary belts that encircled the North American craton (e.g. Palmer 1972, 1974). Elsewhere in North America a pronounced change in slope across this boundary is sometimes evident from slumps and other mass-flow deposits containing shallow-water clasts, typically carbonates, reef and algal debris (e.g. Reinhardt 1977; James 1981; Kepper 1981; Read and Pfeil 1983), but subsequent tectonic disturbance has generally obscured the precise nature of the margin.

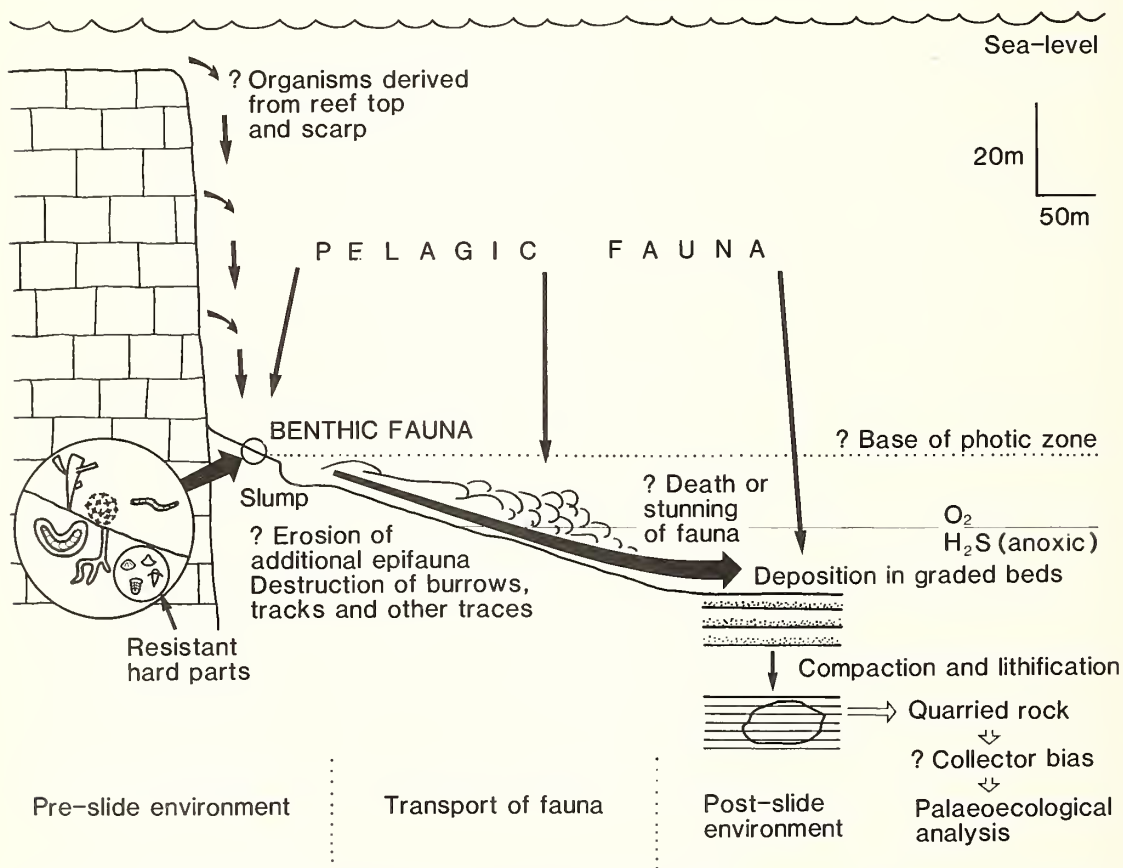
The overall extent of the basin in which the Burgess Shale was deposited is uncertain. General palaeogeographic considerations, however, suggest that the basin and its faunas faced the open sea and would have been accessible to faunal migration. Much of the shelly fauna of the Phyllopod Bed has a wide geographic distribution and none of these genera is endemic to this horizon or the Burgess Shale. For example, amongst the brachiopods and trilobites practically all the genera represented are widespread within North America, and in a number of cases (e.g. *Oryctocephalus*) have an even more extensive distribution (see also Jell 1974). Thus the position of the Burgess Shale, with its indigenous deep-water faunas, argues for a cosmopolitan aspect. Moreover, the abundance of apparently pelagic agnostoid and eodiscoid trilobites is also consistent with open access. In particular *Ptychagnostus praecurrens* has an enormous geographical range (Robison 1982; Bednarczyk 1984) which suggests that potentially the Phyllopod Bed was open to migration from distant parts of the earth.

Evidence is also growing for the existence of faunas broadly comparable to the Burgess Shale elsewhere in the western Cordillera (Utah, Idaho), representing a present-day geographical separation of about 1300 km and a temporal range through a substantial portion of the Middle Cambrian and in some cases probably the upper Lower Cambrian (see Robison 1984). Of approximately forty genera of soft-bodied arthropods, sponges, priapulids, annelids, medusoids, *incertae sedis*, and algae, over 70% are also known from the Burgess Shale (Conway Morris and Robison 1986). Information on soft-bodied faunas from elsewhere in the Middle Cambrian is still restricted, but occurrences in Spain (Liñan 1978; Conway Morris and Robison 1986) and China (Resser 1929) hint at their former distribution.

TAPHONOMY OF THE PHYLLOPOD BED

Introduction

The events that are believed to have led to the preservation of the Phyllopod Bed biota are summarized in text-fig. 1. The benthic fauna was carried and buried catastrophically by turbidity currents (Whittington 1971*a*; Piper 1972), and it is conceivable that biological activity (Hecker 1982) or a high organic content (Keller 1982) contributed to sediment instability. Transport leads to a distinction between the pre-slide environment, where the organisms lived and apparently flourished, and the post-slide environment where inimical conditions helped to ensure the astonishing preservation. The post-slide environment is represented by the Phyllopod Bed, now exposed in the Walcott Quarry. The Phyllopod Bed is located about 20 m from the reef escarpment, and its sequence of graded beds conceivably accumulated in a local sea-floor depression. There is no evidence that the muds bypassed the carbonate shelf via the reef top (Aitken 1971; McIlreath 1977), but there are various clues as to the location of the pre-slide environment in the basin. It appears that many and perhaps all the other



TEXT-FIG. 1. Taphonomy of the Phyllopod Bed (Burgess Shale). The benthic biota inhabiting the pre-slide environment were transported periodically downslope into a presumed anoxic zone, the post-slide environment. The sediment flows carried both living individuals and empty exuviae and shells. The latter would have had a variable residence time in the sediment had they remained in the pre-slide environment; soft parts, however, would have been consumed almost immediately. Pelagic elements were also incorporated, via several possible routes. Subsequent to burial, poorly understood factors that must have included the restriction of microbial decay led to the exceptional preservation. See text for further details.

prolifically fossiliferous localities are located adjacent to the reef scarp, with the abundance of fossils declining sharply away from the reef (McIlreath 1975; Collins *et al.* 1983). If both the pre- and post-slide environments were beside the reef the turbidity currents presumably flowed downslope parallel and adjacent to the reef. Scanty palaeocurrent data from the Phyllopod Bed (Piper 1972) support this hypothesis.

The pre-slide environment

There is circumstantial evidence that the pre-slide environment may have been located near the present day Mount Field. A phase of basin infilling immediately prior to the accumulation of the Phyllopod Bed produced deposition of carbonate flows along a considerable length of the reef-toe; the flows extended some distance away from the Cathedral escarpment and now form the 'Boundary Limestone Unit' (cf. Kepper 1981). In the Mount Field area, however, there is an area of non-deposition adjacent to the escarpment. McIlreath (1977) speculated that this might have been due to either an island on the reef top deflecting carbonate debris as it moved over the rim into the basin, or a local topographic high on the basin floor. Accepting the latter alternative, maintenance of relief until Phyllopod Bed time could have provided a suitable source area from which the turbidity currents originated. The distance between the proposed location of the pre-slide environment in the vicinity of Mount Field and the Walcott Quarry (post-slide environment) is *c.* 0.9–1.8 km. This estimate lies within the range of limiting values calculated by another method, which was based on the separation in depth between the pre-slide (assumed to lie in the photic zone) and post-slide environments, combined with varying values for the angle of slope between the two environments (Conway Morris 1979c).

Some algae, especially *Marpolia* often occur densely strewn on bedding planes with very few metazoans and they may not have grown in direct association with other elements of the pre-slide environment. However, examples of repetitive association, such as that between the algae *Morania* and polychaete *Burgessochaeta* (Conway Morris 1979c), indicate that the pre-slide environment lay within the photic zone, perhaps at a depth of less than 100 m (but see Littler *et al.* 1985). Contrary to Rhoads and Morse (1971), who suggested that the diversity and presence of organisms with hard parts is indicative of well-oxygenated conditions, Savrda *et al.* (1984) and Thompson *et al.* (1985) have shown that such groups occur in modern dysaerobic environments. Although taxonomically very different from Recent faunas, such may conceivably also have been the case in the Phyllopod Bed, and is consistent with the hypothesized proximity of anoxic conditions (see below). Even if the pre-slide environment was dysaerobic, the exceptional conditions promoting soft-part preservation presumably lay in the deeper post-slide environment, and the sea-floor of the pre-slide environment had no unusual preservational properties so that upon death the soft parts of any benthic organisms would have been destroyed quickly by microbial decay and scavenging. In reconstructing the original community it is assumed, therefore, that specimens with soft parts were alive at the time of slumping, because any corpse in the pre-slide environment would have been rapidly consumed. Parts of some animals, however, were more resistant to decay; most significant were the shelly skeletons (trilobites, brachiopods, monoplacophorans, hyolithids) which presumably were largely immune to destruction and had a prolonged residence time in the sediment. There are also species with lightly skeletized parts, especially arthropod carapaces, that persisted after the disappearance of the associated soft tissues. The ratio between intact individuals and those without soft parts in various species (Table 1) is presumably controlled largely by the relative resistance to decay of the lightly skeletized parts. To a lesser extent the ratio will also reflect the species' original abundance (see also Briggs 1978) and, in the case of arthropods, the number of moults. For example, the abundant arthropod *Marrella splendens* consists almost solely of entire specimens, and the rarity of the exuviae (head shields: usually cephalic and lateral spines, more rarely separated) presumably reflects a delicate constitution with a limited resistance to decay and hence a short residence time in the sediment. At the other extreme the arthropods *Tuzoia* spp., *Proboscicaris*, *Isoxys*, *Hurdia*, and *Mollisonia* are known only from their carapaces; this could result from the combination of a relatively tough exoskeleton and original rarity, so that by chance no living specimens were preserved with their soft parts. Other species with

TABLE 1. Abundance and percentage of specimens in eleven genera with lightly skeletized carapaces, headshields, or tubes, lacking their associated soft parts. Totals are estimates based on assumptions of disassociated parts and counterparts (see text).

Genus	Total with soft parts	Total without soft parts	Percentage without soft parts
<i>Canadaspis</i>	4719	4050	46.2
<i>Hurdia</i>	0	128	100.0
<i>Isoxys</i>	0	452	100.0
<i>Marrella</i>	15092	40	0.3
<i>Mollisonia</i>	0	16	100.0
<i>Naraoia</i>	129	168	56.6
<i>Proboscicaris</i>	0	62	100.0
<i>Selkirkia</i>	190	958	83.5
<i>'S.' gracilis</i>	1	37	97.4
<i>Sidneyia</i>	177	132	42.7
<i>Tuzoia</i>	0	37	100.0

a more equitable division between preservational types (Table 1) could represent both moderate original abundance combined with resistance to decay. This observation concerning the post-mortem accumulation of skeletal parts, especially shelly remains, is important because it has biased numerical proportions in the fauna and it is necessary to subtract these vacated hard parts when estimating the total number of organisms alive at the time of slumping, i.e. standing crop. This opportunity to estimate directly the standing crop of a fossil community is normally denied to palaeoecologists, although Kranz (1977) has presented a model for such estimates.

Pelagic elements

Additions to the fauna appear to have come from the pelagic zone. Presumably they include agnostoid and eodiscoid trilobites, groups that are usually interpreted as predominantly pelagic (Jell 1975; Robison 1972, 1975). There is an apparent anomaly in the occurrence of five agnostoids lodged beneath the cephalic doublure of a specimen of the predatory arthropod *Sidneyia inexpectans*, an animal regarded as benthic (Bruton 1981, pl. 13, fig. 99). Some evidence, however, is possibly consistent with the distribution of certain agnostoids being controlled by deeper, cooler water rather than a pelagic existence *per se* (Conway Morris and Rushton, in press). The occurrence of the agnostoid *Ptychagnostus praecurrens* and eodiscoid *Pagetia bootes* in the Phyllopod Bed may reflect the introduction of colder deep waters, perhaps induced by a rise in the thermocline. The Phyllopod Bed fauna could include elements more typical of deeper waters that were able to migrate into relatively shallow water given appropriate conditions.

Whatever doubts surround the life habits of some agnostoid and eodiscoid trilobites, there are also rare soft-bodied species with apparently pelagic adaptations. Presumably, the pelagic animals sank to the sea-bed of the pre- or post-slide environment, or were trapped by one of the turbidity currents (text-fig. 1).

Transport and preferred orientation

The frequency of slumping is not known, although if each graded unit of the Phyllopod Bed represents a separate slump the estimated total of fifty presumably corresponds to this number of events. If the proposed location of the pre-slide environment on a topographic high adjacent to the present Mount Field is correct, then according to McIlreath's (1977, Fig. 1) palaeogeographic reconstruction this would indicate a sea-floor area of perhaps 1 km² from which slumping sampled

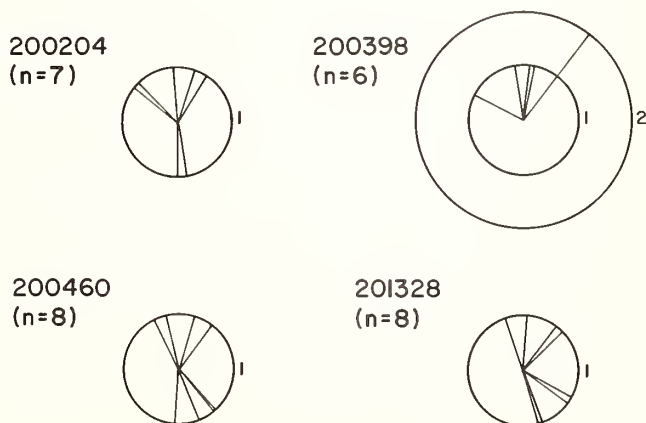
a number of sea-floor sites. Data for this study are taken from the entire Phyllopod Bed and so represent a time-averaged sample of unknown duration (?several decades or centuries).

The presence of an infauna suggests that the bulk of the benthic community was present at the inception of slumping, rather than being swept up by flows descending from a more remote area. The fine grain size (silt-clay) of the sediment and apparently short distance of transport suggest that the erosive power of the turbidity currents was limited. Although some epifauna, nekto-benthos, and stray pelagic organisms may have been incorporated downslope, any infauna probably remained *in situ*. In contrast, where long distance transport of shallow-water faunas occurred, as is inferred from the turbidites of the Pliocene Capistrano Formation of California for example, there was also erosion of deep water infauna (Kern and Wicander 1974).

The fauna was deposited in graded beds with some shelly remains accumulating near the base of a turbidite. The monoplacophoran *Scenella* may form locally dense accumulations with its breviconic shell lying concave side up (Walcott 1912; cf. Piper 1972), a feature also noted in other turbidites (e.g. Middleton 1967). Orientation of other concave-convex fossils has not been studied extensively and is compounded by uncertainty regarding the way-up of collected slabs. Preliminary data, however, indicate that small trilobites have a consistent preference to be one way up (assumed dorsal-to-ventral ratio is 1:2.3–3.9), whereas the larger *Olenoides serratus* has a more or less equal distribution. In contrast, Cisne (1973b) recorded no way-up preference in the small Ordovician trilobite *Triarthrus* entombed in the microturbidite of Beecher's Trilobite Bed. Soft-bodied animals were deposited in a wide variety of orientations, including some individuals with their longitudinal axes either steeply or vertically inclined to the bedding (Whittington 1971a), while compressed worms such as *Pikaia* (chordate) and *Louisella* (priapulid) may be folded or otherwise contorted (Conway Morris 1977a, 1979a). The reduction of the Phyllopod Bed collections to thousands of unoriented sawn slabs, each with only one or a few specimens, has removed a potentially valuable source of information regarding non-random distributions, but some evidence exists for preferred orientation of elongate specimens (cf. Cisne 1973b). In vacated tubes of *Selkirkia columbia* (priapulid) there is evidence of bimodal and more rarely unimodal distributions (text-fig. 2), although the samples are small. Amongst the agnostoid and eodiscoid trilobites (text-fig. 3) a χ^2 test indicates that their distributions are not significantly different from uniform. This may also be true for one sample of the larger trilobite *Olenoides* (un-numbered USNM slab), but in USNM 189800 the distribution appears to be bimodal (text-fig. 3).

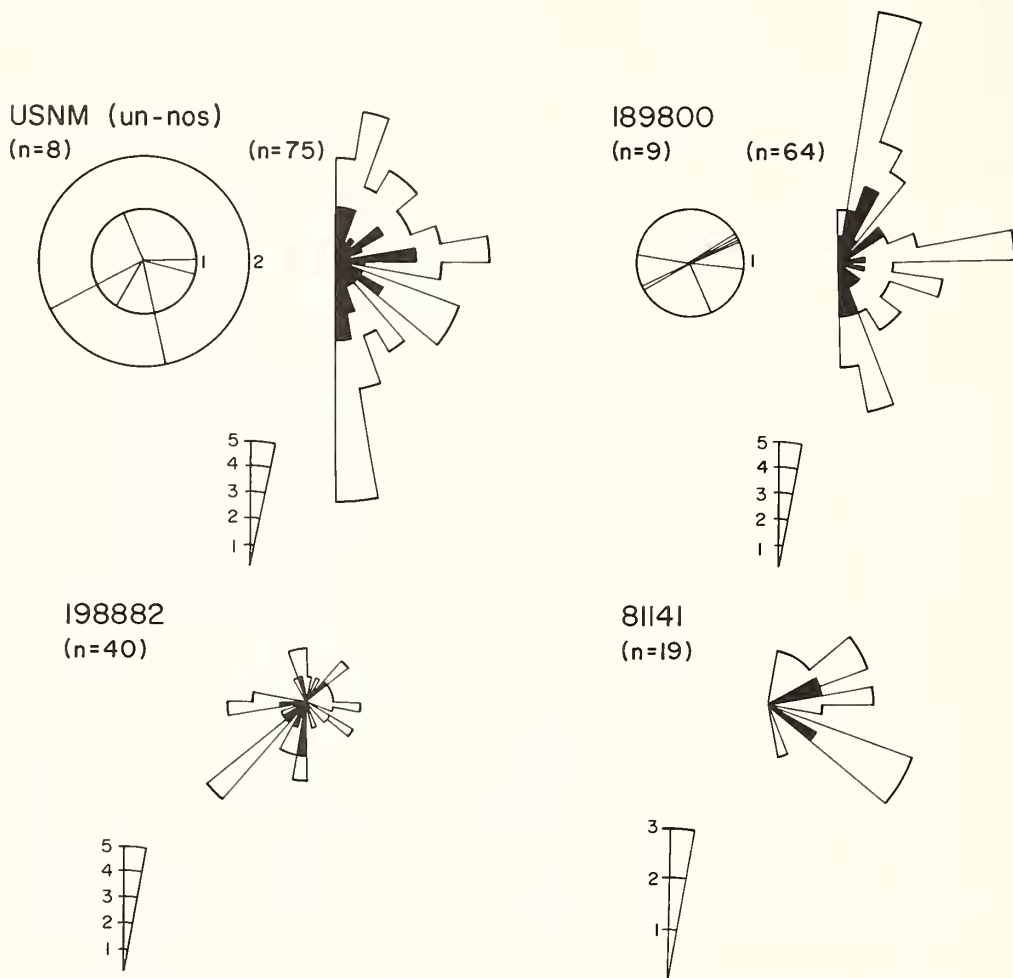
The post-slide environment

The presence in the post-slide environment of anoxic conditions, perhaps due to hydrogen sulphide extending above the sediment-water interface (text-fig. 1), is inferred from the absence of either



TEXT-FIG. 2. Rose diagrams showing varying extent of preferred orientation in the tubicolous priapulid *Selkirkia columbia* on Phyllopod Bed (Burgess Shale) slabs; true North not known. USNM specimen numbers given; azimuth direction towards anterior aperture; no soft parts present.

scavenging or bioturbation. Rare pyrite-filled structures (text-fig. 4a) may represent gas-generated hollows in the sediment (see Cloud 1960; Martens 1976) rather than metazoan burrows. To judge by the general restriction of prolific faunas to the basinal margins beside the escarpment (McIlreath 1974, 1977), anoxia may have been a regional feature of the deeper waters of the basin. In addition to anoxic conditions, rapid burial was presumably an important factor in promoting exceptional



TEXT-FIG. 3. Rose diagrams showing varying extent of preferred orientation in trilobites on Phyllopod Bed (Burgess Shale) slabs; true North not known. USNM un-numbered slab, left-hand rose, *Olenoides serratus*, azimuth direction towards anterior (5 individuals dorsal-up, 3 ventral-up, 7 or possibly 8 with soft parts); right-hand rose, *O. serratus*, azimuth direction towards anterior (4 individuals dorsal-up, 5 ventral-up, 8 or possibly 9 with soft parts); right-hand rose, agnostoids, no azimuth distinction between anterior and posterior (52 individuals dorsal-up, 23 ventral-up (black), 36 complete, 39 incomplete). USNM 189800, left-hand rose, *O. serratus*, azimuth direction towards anterior (4 individuals dorsal-up, 5 ventral-up, 8 or possibly 9 with soft parts); right-hand rose, agnostoids, no azimuth distinction between anterior and posterior (46 individuals dorsal-up, 18 ventral-up (black), 37 complete, 27 incomplete). USNM 198882, *Pagetia bootes*, azimuth direction towards anterior (32 individuals dorsal-up, 8 ventral-up, 1 lateral). GSC 81141 (= 35.5 cm above base of Phyllopod Bed), agnostoids, no azimuth distinction between anterior and posterior (15 individuals dorsal-up, 4 ventral-up (black), 18 complete, 1 incomplete).

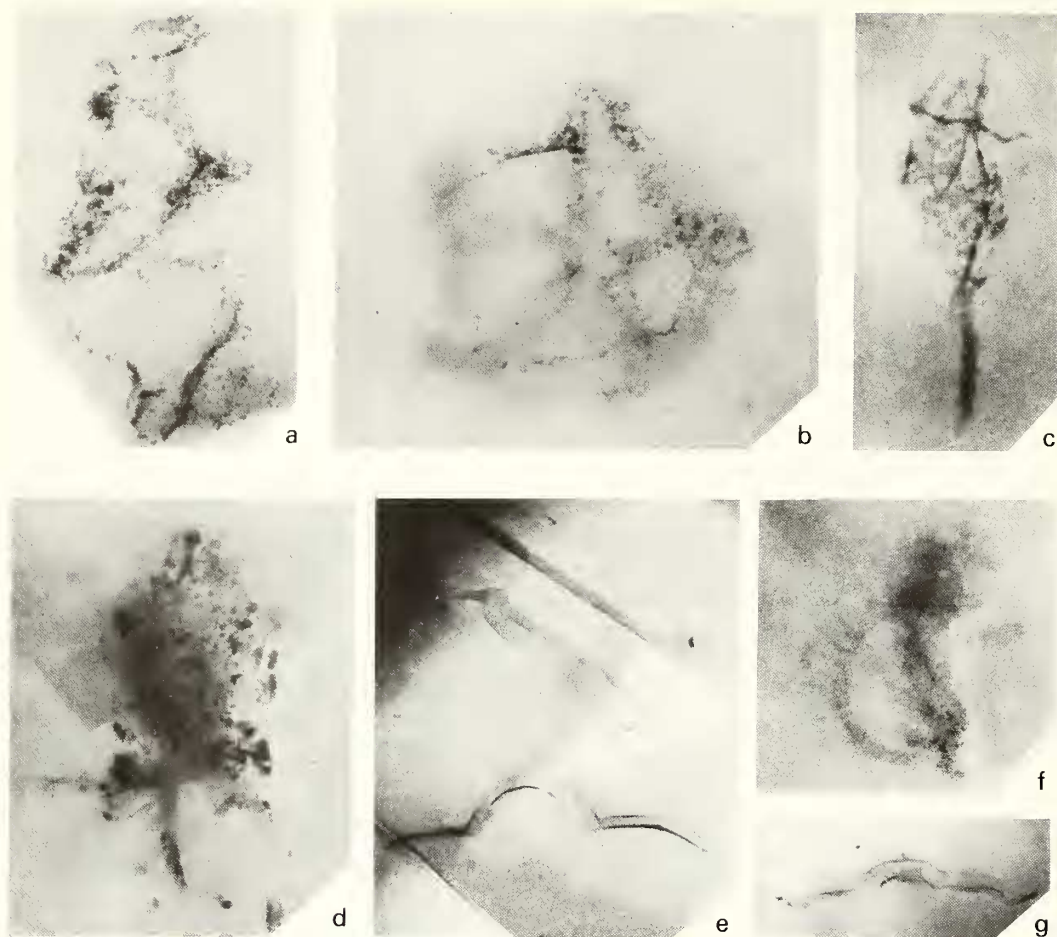
preservation (cf. e.g. Goldring and Stephenson 1972; Liddell 1975). Experiments and observations on the depth of overburden necessary to immobilize various benthic taxa in modern marine environments (e.g. Schäfer 1972; Kranz 1974; Nichols *et al.* 1978) and some ancient settings (e.g. Hardy and Broadhurst 1978) may only be broadly indicative considering the taxonomic distinctiveness of the Phyllopod Bed fauna. Presumably all sessile organisms, especially sponges and echinoderms, and an appreciable portion of the vagrant epifauna had limited escape abilities after burial, but the absence of escape structure associated with the priapulids that were evidently effective burrowers (Conway Morris 1977a) suggests that the fauna was either stunned or even dead on arrival at the post-slide environment. The latter condition is indicated by an apparent lack of response to anoxic conditions; some modern annelids and arthropods combat an anoxic milieu by entering metabolic stasis and coiling tightly (Dean *et al.* 1964), but such a feature is infrequent amongst Phyllopod Bed specimens. Reasons for death are speculative, but if the pre- and post-slide environments were separated by a temperature boundary then the fauna may have perished owing to thermal shock. In this context it may be significant that elevated water temperatures have been recorded during the introduction of a storm-generated turbidite into deeper water (Dengler *et al.* 1984). Osmotic shock promoted by transport through an equivalent pycnocline generated by salinity differences may be considered less likely because soft-bodied specimens show neither conspicuous ballooning nor wrinkling attributable to osmosis-induced shrinkage, although such features have been documented in other exceptional fossil faunas (e.g. Barthel 1970; Müller 1985).

Living metazoans appear to have been absent from the post-slide environment, but the post-slide environment was not sterile as anaerobic bacteria were presumably present and responsible for the incipient rotting noted in many specimens (e.g. Conway Morris 1977a, 1979c). A conspicuous feature of decay in some species is a dark organic patch beside the specimen; in some specimens of *Marrella* this stain has been observed to extend at least 20 mm from the body, suggesting that during its diffusion or flow in the early stages of decay, the surrounding sediment was wet and had a high porosity. Some Recent marine animals (decapod crustaceans) exude a brownish fluid when subjected to pressure changes (Menzies and Wilson 1961), but the presumably modest change in water pressure (7.2 kg/cm² for a 70 m vertical displacement: see Conway Morris 1979c) between the pre- and post-slide environments would probably have been insufficient either to kill the fauna or expel body contents. Decay was only preliminary, and one or more factors evidently intervened before it was far advanced. In modern marine sediments bacterial populations, including anaerobics, often decline markedly beneath the sediment-water interface (e.g. Zobell 1938, 1942; Rittenberg 1940; Oppenheimer 1960; Marty 1981). Progressive burial beneath a series of graded beds may have diminished bacterial numbers so drastically as to render their activity on buried organic matter ineffective. More speculatively, appeals could be made to abrupt decrease in water content (early lithification) or changes in salinity (K. M. Towe, pers. comm.) to render anaerobic bacteria inoperative.

Diagenesis

Whatever mechanism was responsible for the termination of decay the buried organisms were presumably reduced to carbon-rich remains relatively shortly after burial. The soft parts of fossils, however, do not appear to be carbonaceous, but consist of aluminosilicate films (Conway Morris 1977a). Reflective areas of these films are said to be composed of muscovite mica (K. M. Towe, pers. comm.). The exoskeleton of the trilobite *Olenoides* has been replaced by various minerals including chlorite and mica (Conway Morris and Pye, unpublished; see also Whittington 1980b), and other shelly remains that were originally calcareous and soft-bodied material both appear to have a broadly similar composition. The time and rate of transition of the fossils to phyllosilicates is speculative, but may have occurred at depth under fairly elevated temperatures and pressures, coincident with the pronounced compaction noted by various authors (Rasetti 1966; Whittington 1975a, b; Robison 1982).

Pyrite occurs in association with many specimens, and is usually in the form of framboids (Conway Morris 1985a); pyrite formation is probably linked with the activity of anaerobic bacteria (Bubela



TEXT-FIG. 4. Radiographs of Phyllopod Bed (Burgess Shale) fossils showing pyritization. *a*, UM 1320, irregular pyritic structure, possibly representing original gas generated hollows, $\times 1.7$; *b*, GSC 45368, edrioasteroid *Walcottidiscus* sp. in aboral view, $\times 2.7$; *c*, *d*, GSC 45369, an eocrinoid, probably *Gogia? radiata* (see Sprinkle 1973), $\times 2.0$; *c*, part with ridged plates and incomplete stem, *d*, counterpart with enigmatic branching structure associated with lower region of calyx; *e*, GSC 45370, isolated thoracic segments of trilobites, $\times 1.8$; *f*, GSC 78452, problematical organism, possibly an echinoderm, $\times 1.8$; *g*, GSC 78453, thoracic trilobite segment, $\times 1.0$.

GSC, Geological Survey of Canada, Ottawa; UM, University of Montana, Missoula.

and Cloud 1983). In some cases, however, the pyrite has replaced the fossil rather than formed a framboidal coating. This partial replacement appears to have been largely restricted to hard parts, including those of echinoderms (text-fig. 4*b-d*), trilobites (text-fig. 4*e, g*), problematical remains (text-fig. 4*f*), and sponge spicules (see Walcott 1920). One echinoderm (text-fig. 4*c*) which appears to be referable to *Gogia? radiata* (see Sprinkle 1973) is of particular interest. The part is moderately well preserved, with an incomplete stem (if comparisons with *G.? radiata* are valid) and remains of the radiating ridged plates. The counterpart is more poorly preserved, although there is a fairly clear indication that some of the calyx plates have epispires. More enigmatic is a prominent branching structure, adjacent to the stem, that could be interpreted as the brachioles. It is located beside the proximal calyx, however, and folding of the brachioles into this position is unlikely; unless the brachioles became detached, chance superposition with some other structure is perhaps more likely.

Concluding remarks

Exceptional fossil preservation gradually dies out above the Phyllopod Bed, and this decline could be linked to the cessation of conditions of rapid burial by turbidity currents. The final stage in the taphonomic history, that of quarrying and collection, has been summarized elsewhere (Whittington 1971a, 1980a; Conway Morris 1982). Measurements of the dimensions of the Walcott Quarry indicate that c. 600 m³ of Phyllopod Bed were removed. Discarded material forms a thick talus on the slopes below the quarry and, together with debris from Walcott's camp, has provided an additional source of specimens to later collectors (Collins 1978). The extent of collection bias is not certain. In the USNM the large size and relative inferiority of some of the specimens suggests Walcott was not unduly selective. Collecting by the Geological Survey of Canada appears to have been reasonably thorough.

SOURCES OF DATA

Locations of specimens

The data of specimen counts on the collected slabs come from several sources. By far the most important is the enormous collection made by Walcott during five seasons (1910–1913, 1917) of field-work and now stored in the National Museum of Natural History, formerly the United States National Museum (USNM), Smithsonian Institution. Phyllopod Bed specimens are usually labelled 35k, while the much smaller number of specimens (c. 465) from a higher excavation (apparently the same as Raymond Quarry: see Whittington 1971a) are labelled 35k/10 or 35k/1. When the labels are absent the provenance can usually be determined by the lithology. Two seasons (1966, 1967) of excavations by the Geological Survey of Canada (GSC) produced a smaller sample, approximately 11% of the estimated USNM total. A number of museums and university departments possess small Burgess Shale holdings (Appendix 1), the majority of which were either exchanged or purchased from the Smithsonian and are mostly included here with the USNM totals. In 1975 the Royal Ontario Museum, Toronto (ROM), collected fossils from the talus discarded by previous expeditions. With the exception of a few undoubted Phyllopod Bed specimens this material is excluded because the exact provenance is not certain.

For the purposes of this paper specimens from all levels of the Phyllopod Bed are considered together. This is because, although the GSC recorded the vertical distribution of specimens, the measured divisions usually encompass a number of turbidite horizons, while Walcott (1912) offered only a few meagre hints at an early stage of his collecting. Thus, while the GSC data show abundance of various species to vary through the Phyllopod Bed (see Conway Morris 1985a), the ideal case of assessing separately the contents of each slump is not feasible and the fauna is a time-averaged assemblage (Walker and Bambach 1971). As noted above, however, there appears to have been only one benthic community in the pre-slide environment and, while an individual slump would be unlikely to trap representatives of the entire fauna, multiple slumping of various portions of the sea-floor increased the probability of assessing its overall diversity. Such successive temporal sampling is thus presumably analogous to the sampling of a modern benthic community by a series of sediment grabs or a towed sledge.

Problems in estimating numbers of individuals

Burgess Shale specimens adhere to both sides of the split rock, so giving parts and counterparts. It is important that part and counterpart be kept together because the level of splitting through the specimens often varies and may confine certain features to either part or counterpart (e.g. Whittington 1975a; Conway Morris 1979c, 1985a). Walcott apparently failed to appreciate this, and in the USNM collections c. 95% of specimens are presently disassociated. Part and counterpart may be stored in separate drawers. Alternatively, one side either may never have been collected or was even sent to another institution. Using several species where the totals of parts only and parts plus counterparts are known, it is estimated that in the USNM collections approximately 75% of specimens are unassociated parts while the other 25% are disassociated parts and counterparts.

Independent support for these estimates comes from a comparison in the tubicolous priapulid *Selkirkia* of the relative proportion of vacated tubes to those with associated soft parts (Conway Morris 1977a). In the GSC collections the proportion of specimens with soft parts is known to be *c.* 21% with reasonable confidence because a careful attempt was made to find all parts and counterparts. In the USNM sample of this priapulid, that is about six times larger, the same proportion is calculated on the basis of the figures given above to be *c.* 19%.

During the GSC collecting a point was made to keep parts and counterparts together and *c.* 25% of specimens are presently associated. Although some counterparts were never collected, some disassociation has occurred in the GSC material. In the majority (66%) of cases where only the part is known it is supposed that the counterpart is not available, but in the remaining 34% of specimens inadvertent disassociation is assumed. If these correcting factors, which are used as the basis of this paper's analysis, are accepted, the original proportion of associated USNM specimens was *c.* 19%, whereas in the GSC sample the figure is approximately 42%.

The Phyllopod Bed collections used in this study are located on a total of about 33 520 slabs, of which about 3400 consist of associated parts and counterparts. Using the correcting factors given above for disassociated parts and counterparts in the USNM and GSC collections, the original total of slabs (parts only, parts and counterparts) is believed to be approximately 29 700 slabs. I estimate to have inspected directly *c.* 97% of the slabs, so that any bias should be consistent. Data for the remaining 3% of slabs were supplied from specimen lists of various institutions' holdings. Each slab (both sides) had a note made of its specimens (average 2.5 specimens/slab), both for counts of individuals and intra- or interspecific associations. On large slabs crowded with specimens only estimates were made, especially for *Canadaspis perfecta* that occurs as 'herds' of intermingled soft-part specimens and isolated carapaces (Briggs 1978), and dense tangled knots that, although poorly preserved, appear to represent specimens of the worm '*Ottoia*' *tenuis*. Specimens concealed entirely within slabs escape notice, and even radiography would fail to reveal buried specimens whose silicate films have minimal density contrast with the surrounding matrix. The thinness of most slabs, however, combined with preferential splitting through fossil films (Conway Morris 1979c) suggests that this is not a serious source of error.

Numbers of individuals

It is calculated, therefore, that the available sample consists of about 73 300 specimens (of which the USNM component accounts for *c.* 89%), distributed as follows: animals 87.9%, algae 11.3%, and indeterminate material 0.8%. The algal (see Walcott 1919; Satterthwaite 1976) count is very approximate as each slab with abundant coverings, especially of *Marpolia spissa* and *Morania confluens*, was registered as a single specimen. The total for the indeterminate category is also only a rough guide. These two categories are not considered in any further detail; the remainder of this paper assesses the animal component and in particular that fraction judged to have been alive at the time of slumping (estimated 40 368 specimens). As noted above, it is necessary to distinguish between individuals alive at the time of transport and those dead specimens, or parts thereof, that persisted in the sediment owing to a resistant skeleton. The live:dead ratio within shelly species of modern communities has received wide attention (e.g. Macdonald 1976) because of its palaeoecological applications. The Phyllopod Bed fauna offers a most unusual opportunity for at least partial inspection of this problem. In some species with hard parts it is possible to distinguish live from dead specimens, even when soft tissue is not apparent. In *Hyolithes*, helens and operculum attached to the conical shell are good evidence for vitality. Mantle setae protruding from the valves of *Micromitra* are similarly interpreted as evidence of the specimens being alive during transport. Such criteria, however, are not available in the monoplacophorans, represented almost entirely by *Scenella*, and most of the brachiopods. The proportion of live to dead individuals is arbitrarily taken as 5% for monoplacophorans (same as *Hyolithes*) and 14% for brachiopods (same as *Micromitra*).

Biovolumes

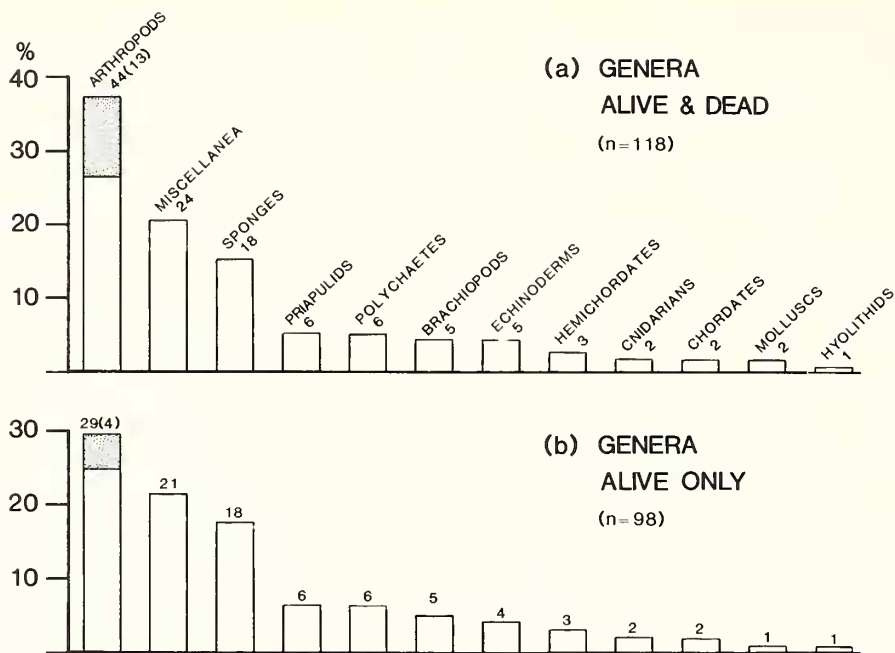
In addition to specimen counts, biovolumes were calculated for each genus that had representatives

living at the time of transport. Estimates were made by reference to an individual of average length, and then multiplied by the specimen total to give the population's biovolume. Simple formulae for standard shapes were used. Calculation of biovolumes in cylindrical worms such as priapulids was straightforward, but in more complex organisms (e.g. an arthropod) the body was treated as a number of separate units. In these calculations no allowance (as biomass) was made for skeletal hard parts, but serious discrepancies are unlikely because groups with hard parts were not an important part of the original community (see below). Not surprisingly, despite the wealth of palaeocommunity studies, use of biovolume measurements in palaeoecology has been rather limited (e.g. Walker 1972*a, b*; Fürsich and Wendt 1977; Stanton *et al.* 1981; Dzik 1979; Wiedman 1983, 1985) given the nature of the material (see Duff 1975). Nevertheless, they correspond approximately to original biomass and so provide a crude estimate of relative production and standing crop. These biovolumes reflect in some way the energy expended in growth. As Stanton *et al.* (1981; see also Powell and Stanton 1985) pointed out, however, when assessing biovolumes of carnivorous gastropods in an Eocene assemblage, no account is taken of energy expended in maintenance (respiration, excretion); these authors' attempts to estimate a time-related cumulative biomass (as biovolume), while praiseworthy, were based on a number of assumptions that make any application to this study practically impossible. In any event, biovolumes may be a better guide to relative ecological importance than numbers of individuals (see also Staff *et al.* 1985) because of size variation between species, from a few mm (e.g. *Lecythioscopa*) to over 300 mm long (e.g. *Anomalocaris*, *Tegopelte*), although in his study of a modern community Sanders (1960) considered numbers to be more reliable than biomass estimates because only a few, large, randomly distributed animals may alter radically the measured values. The ratio between smallest and largest calculated biovolumes in average-sized specimens is several orders of magnitude. Comparing biovolumes between the major groups, however, is a very questionable exercise because of the range of body plans involved: sponges and cnidarians, with extensive water- and mesoglea-filled interiors respectively; priapulids, with spacious body cavities; and arthropods, with haemocoels and almost invariably at least a lightly skeletized exoskeleton. Intragroup comparisons of biovolumes, however, may be more valid.

ANALYSIS OF THE FAUNA

Numbers of genera, individuals, and biovolumes

Genera. Several estimates are available of the composition of the entire Burgess Shale fauna in terms of numbers of genera, most of which are monospecific, within the principal groups (e.g. Conway Morris 1979*a, b*; Conway Morris and Whittington 1979; Whittington 1980*a*). The present compilation (text-fig. 5) refers to the Phyllopod Bed only and excludes the few genera (*Carnarvon* (Walcott 1912), *Priscansermarinus* (Collins and Rudkin 1981), *Scolecifurca* (Conway Morris 1977*a*)) restricted to beds above the Walcott Quarry. Values given for all genera in text-fig. 5*a* differ little from earlier estimates. Text-fig. 5*b* shows the relative numbers of genera that had living representatives at the time of transport. It excludes those genera, mostly arthropods, known only from exuviae or other resistant parts lacking soft tissues. Apart from the decreased importance of the arthropods (especially trilobites) when only living genera are considered, comparisons of generic abundance in the two histograms (text-fig. 5*a, b*) show a broadly similar order of importance. It should be emphasized that only c. 14% of the genera with preserved soft parts have shelly skeletons (excluding sponges, that would disaggregate into widely dispersed spicules) capable of being fossilized in normal circumstances, although this value rises to approximately 20% when genera known only from exuviae or empty shells are included. An absence of soft-part preservation is particularly conspicuous in the polymeroid trilobites. Only four genera have soft parts recorded (*Kootenia*, *Elrathina*, *Elhmaniella*, *Olenoides*), and practically all (97%) are specimens of *Olenoides*. Judging by these samples the soft parts in the other trilobites are unlikely to have been entirely concealed; the erratic distribution of soft-part preservation may be due in part either to original rarity of most trilobite genera combined with a prolonged residence time of the empty exoskeletons in the pre-slide sediments, or their

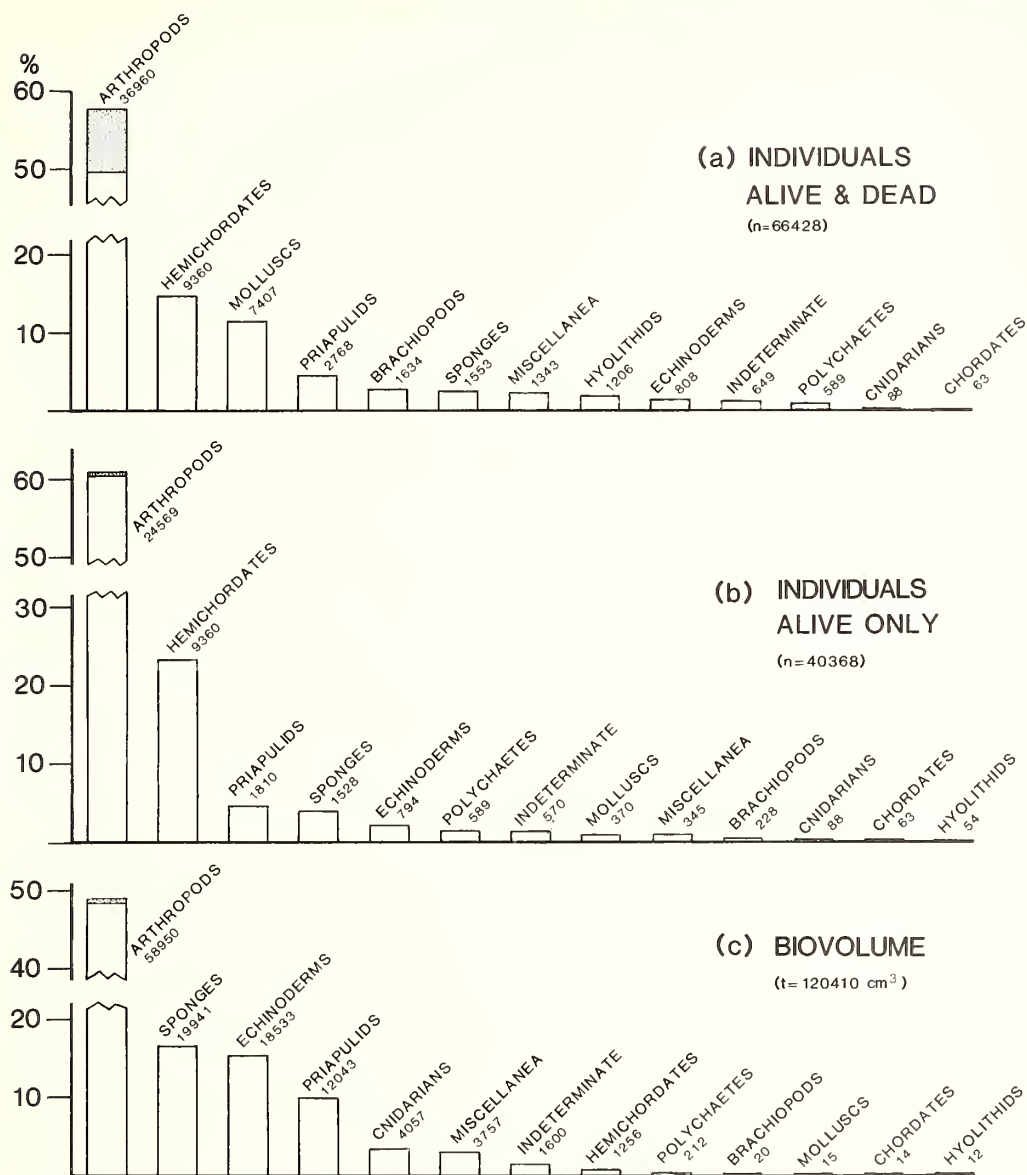


TEXT-FIG. 5. Relative percentages of the Phyllopod Bed (Burgess Shale) fauna in terms of numbers of genera (mostly monospecific) within each major group. *a*, genera with living representatives at time of burial plus genera represented by vacated shells and exuviae; *b*, genera with living representatives only. Stippled portion of arthropod bar refers to proportion of trilobites.

post-mortem introduction from elsewhere, which would reduce even further their importance in the standing crop of the pre-slide community. The former proposal, however, does not readily explain the high ratio (*c.* 0.8: 1.0) between living specimens and unexpectedly rare intact exuviae of *Olenoides*, unless the exoskeleton of this large trilobite was particularly susceptible to destruction by premoult demineralization or by benthic scavengers.

In comparison, Cisne (1973*a*) recorded a similar live to dead ratio in specimens of the Ordovician trilobite *Triarthrus eatoni* from the celebrated Beecher's Trilobite Bed, New York. His census included, however, fragmentary material and, in addition, practically all the protaspids and meraspids were represented only by exuviae. Accordingly, Cisne (1973*b*) regarded almost 99% of the holaspid specimens as being alive immediately before burial. An analogous problem exists in the Devonian (Emsian) Hunsrückschiefer of West Germany, where soft-part preservation occurs in a number of trilobites including *Phacops* and '*Asteropyge*', but not in *Parahomalonotus*. In this instance Brassel and Bergström (1978) suggested that the potential for soft-part preservation was controlled by the position relative to the sediment-water interface. The infaunal *Parahomalonotus* is believed to have been capable of emerging subsequent to rapid burial, unlike the epifaunal *Phacops* and '*Asteropyge*', while if individuals of the former genus died in their burrows the openness of their domiciles would promote rapid decay. However, in *Phacops* and '*Asteropyge*' soft-parts are known only in *c.* 10% of individuals.

Individuals. The relative importance of the principal groups in terms of numbers of individuals is shown in text-fig. 6*a, b*, again distinguishing between all specimens and only those individuals alive during transport. Arthropods predominate, while the important role of hemichordates results from the estimated abundance (see sources of data) of '*Ottoia tenuis* (Walcott 1911*b*) which is unrelated to the type species *O. prolifica* (Priapulida) (Conway Morris 1977*a*). '*O.*' *tenuis* has a bulbous anterior



TEXT-FIG. 6. Relative percentages of the Phyllopod Bed (Burgess Shale) fauna in terms of numbers of individuals and biovolumes of the major groups. *a*, individuals with living representatives at time of burial plus specimens represented by vacated shells and exuviae; *b*, individuals with living representatives only; *c*, calculated total biovolumes of each group. Stippled portions of arthropod bars refer to proportion of trilobites, and in *b* and *c* have been exaggerated for the purposes of clarity (see text).

attached to an elongate trunk by a narrow stalk, an appearance which is reminiscent of hemichordate enteropneusts (unpublished observations). In the living fauna (text-fig. 6*b*) the remaining groups are relatively insignificant with none accounting for more than 4.5% of the total. A striking feature emerges in comparing the shelly components (trilobites, molluscs, brachiopods, very rare echinoderms): in text-fig. 6*a* they are fairly conspicuous, whereas in text-fig. 6*b* these groups are

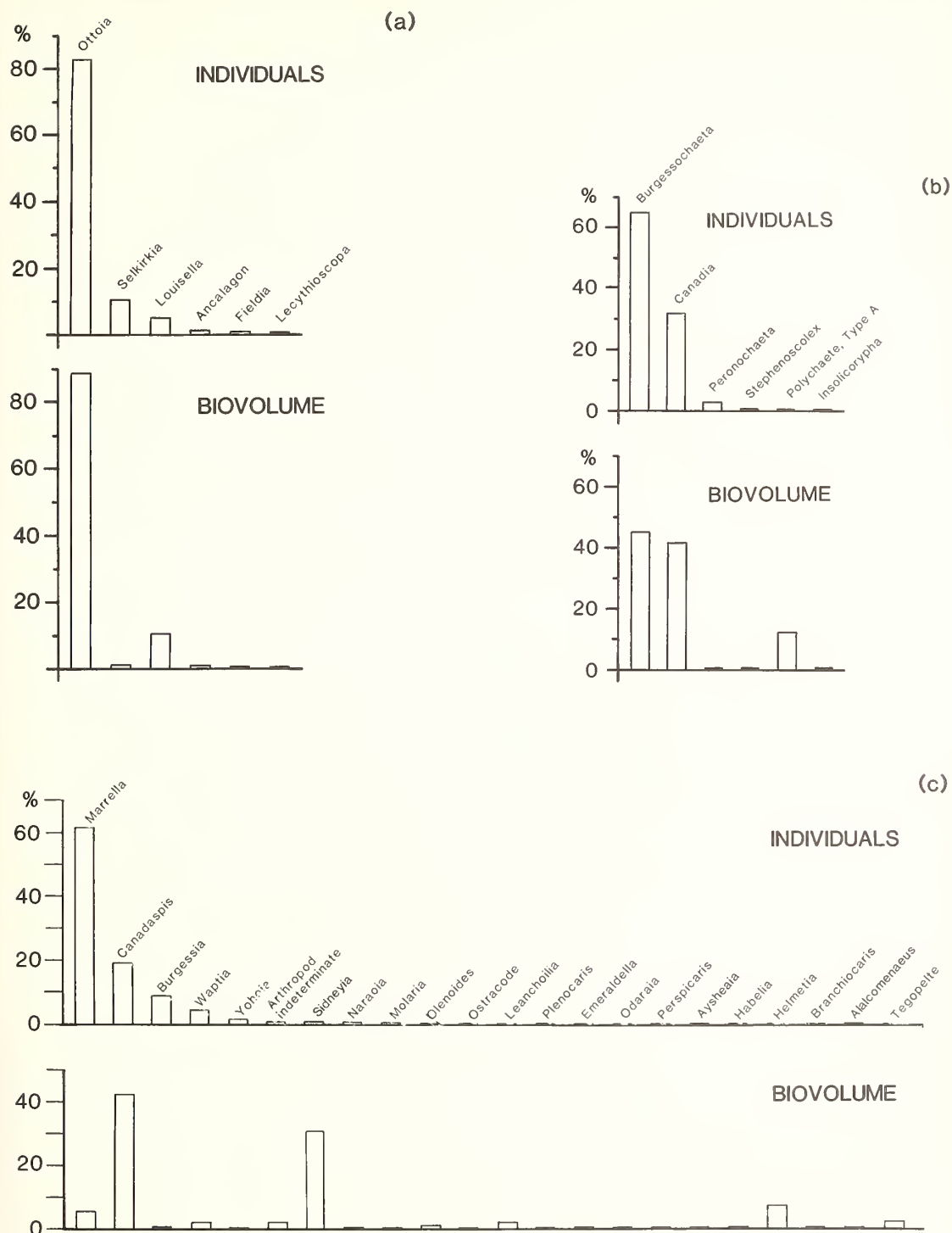
insignificant. Their exact proportions in the living community are dependent on various assumptions (see sources of data), but our notion of the Phyllopod Bed community and its ecology, and by implication some other Cambrian faunas, would be seriously warped if it had to be based solely on shelly fossils. Thus, if these figures are taken to be correct, only *c.* 2% of individuals (excluding sponges) alive at the time of burial had hard parts capable of fossilization in normal taphonomic circumstances. Even if it were assumed that half the shelly component assigned to the 'dead' category was actually alive at the time of burial (a rather optimistic assumption given the likely residence time of empty shells and exuviae in the sediment), then their proportion of the standing crop in terms of individuals would be only about 12%. Such estimates take on special significance amongst the trilobites, as this group dominates most Cambrian assemblages. In the Phyllopod Bed community trilobites with robust skeletons (excluding *Naraoia* and *Tegopelte*: see Whittington 1977, 1985) account for less than 0.5% of all arthropod individuals alive at the time of burial (text-fig. 6b) and a correspondingly smaller fraction of the entire fauna. Even if estimates of trilobites alive at the time of burial are taken to include all intact exuviae (excluding presumed pelagic agnostoids and eodiscoids) the proportion of trilobites within the arthropod assemblage would fall short of 5%.

Biovolumes. Text-fig. 6c depicts the relative biovolumes of the major groups. Arthropods maintain their pre-eminence, but in parallel with numbers of individuals the estimated percentage biovolume of trilobites within the arthropods is a trivial 1%. The small size of '*O.* *temuis*' greatly reduces the significance of the hemichordates in comparison with numbers of individuals. The sponges and priapulids account for an appreciable fraction of the total biovolume as both are fairly numerous and large. The importance of the echinoderms is due to the medusoid-like *Eldonia*. Following Durham (1974) this organism is presently regarded as a holothurian, although a detailed redescription may well support Paul and Smith's (1984, p. 496) reservations regarding its echinoderm affinities. Various comparisons between the major groups should be noted (text-fig. 6). For example, apart from the recurrent importance of arthropods, it is worth emphasizing that although the Miscellanea (which includes a number of bizarre species that if found today would probably be regarded as new phyla: see Conway Morris 1985b) and chordates have attracted wide interest, they are of rather minor significance in terms of individuals (text-fig. 6b) and biovolume (text-fig. 6c).

Comparisons of individuals and biovolumes. Three groups (arthropods, priapulids, polychaetes) are analysed in more detail with respect to numbers of individuals and biovolumes to see whether these alternative methods of assessing relative importance give compatible results (text-fig. 7). Intragroup comparisons of biovolume may be reasonably valid because of overall similarity in body architecture. In the priapulids (text-fig. 7a) and polychaetes (text-fig. 7b) the distribution of numbers of individuals and biovolumes is fairly concordant, whereas wide discrepancies occur in the arthropods (text-fig. 7c) where large, relatively uncommon genera, e.g. *Sidneyia* (estimated 177 individuals with associated soft parts), outweigh in terms of biovolume far more numerous but smaller forms such as *Marrella* and *Burgessia* (estimated 15092 and 2158 individuals).

Ecology: life habits

Introduction. The ecology of the Phyllopod Bed fauna is assessed here in terms of life habits and trophic groups, both of which are divisible into a number of categories (Table 2) based on standard schemes of palaeoecological classification (e.g. Scott 1972, 1978; Walker 1972a; Walker and Bambach 1974; West 1977). With a few exceptions, such as symbiotic associations (?commensalism) between brachiopods and sponges (Conway Morris 1977a, 1982; Whittington 1980a) and possibly *Wiwaxia* (Conway Morris 1985a), direct evidence of life habits (position relative to the water-sediment interface, tracks, burrows, and other traces) has been destroyed as a result of transport (text-fig. 1). Each genus is assigned a life habit, and those of some groups can be inferred with reasonable assurance. For example, all sponges and brachiopods are regarded as sessile epifauna even though some Cambrian inarticulate brachiopods were evidently infaunal (Pemberton and Kobluk 1978).



TEXT-FIG. 7. Comparison of numbers of individuals alive at the time of burial and biovolume in genera of three major groups in the Phyllopod Bed (Burgess Shale). *a*, priapulids; *b*, polychaetes; *c*, arthropods.

TABLE 2. Ecological classification used for the Phyllopod Bed fauna.

Life habit	Code	Feeding type	Code
Infaunal, sessile	IS	Suspension, undifferentiated	SU
Infaunal, vagrant	IV	Suspension, high level (c. > 10 mm)	SU ^H
Epifaunal, sessile	ES	Suspension, low level (c. < 10 mm)	SU ^L
Epifaunal, vagrant	EV	Deposit, collector	DC
Nektobenthic	NK	Deposit, swallower	DS
Pelagic, floater	PF	Carnivores/scavengers	PC
Pelagic, swimmer	PS	Unknown	UN
Unknown	UN		

Benthos. Considerable uncertainty surrounds the life habits of the arthropods, which are mostly classified as vagrant epifauna (see also Briggs and Whittington 1985). The extent of infaunal activities amongst the arthropods is conjectural and has only been briefly discussed for a few forms, e.g. *Burgessia* (Hughes 1975). Other epifaunal animals evidently included *Wiwaxia* as an adult, although juveniles may have been infaunal (Conway Morris 1985a), and some of the genera of *Miscellanea*. This latter group includes *Hallucigenia* which appears to have supported its body and walked on seven pairs of sharply pointed stilt-like appendages that lacked 'snow-shoe' adaptations (see Thayer 1975) and which are comparable, for instance, to the distal rosettes of spines found in arthropods that patrolled the soft substrates of the Devonian Hunsrückschiefer (e.g. Seilacher 1962; Stürmer and Bergström 1978). While the phyletic relationships of *Hallucigenia* are obscure (Conway Morris 1977b), ecological analogues apparently exist. They include the tripod fish (*Bathypterois* and its relatives) that rests on the sea-bed with the aid of enormously elongate spines arising from the tail and pectoral fins; pycnogonoids; and elasipod holothurians, e.g. *Scotoplanes*, that support their bodies on the tips of their tube-feet (e.g. Barham *et al.* 1967; Heezen and Hollister 1971; Herring and Clark 1971; Lemche *et al.* 1976). *Hallucigenia* was presumably very close to neutral buoyancy, and locomotion over muddy substrates must have been feasible unless there was a deep layer of flocculent material. On the basis of its calculated biomass, M. LaBarbera (pers. comm.) has suggested that *Hallucigenia* would only be stable in areas of very low current velocity (< 2.5 m/s) unless it had additional means, e.g. its tentacles, of securing itself. In this context, it is interesting to note that elasipod holothurians are swept off their podia and tumbled about by the movement of a passing bathyscape, indicating that they too have only very slight negative buoyancy (Barham *et al.* 1967).

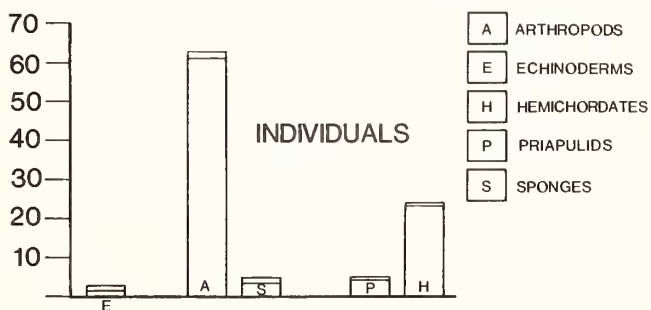
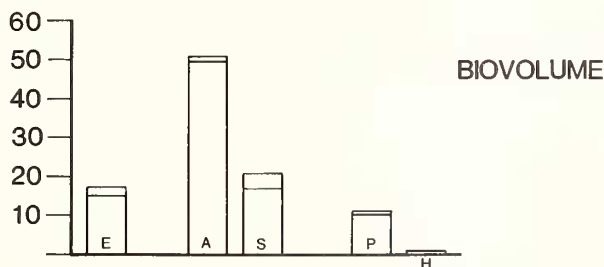
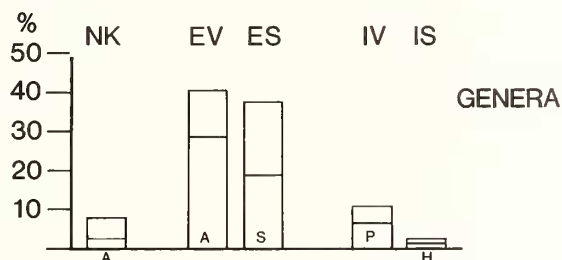
Amongst the infauna, all the priapulids apparently burrowed but some species may have made at least occasional excursions over the sea-bed in the same manner as modern priapulids (Menzies *et al.* 1973, fig. 7-15F). Furthermore, the priapulid *Louisella* may have been more sedentary. Its dorsoventrally compressed body with two rows of gill papillae along much of its trunk finds an analogy with some eunicid polychaetes which occupy horizontal burrows and drive respiratory currents over the gills by dorsoventral undulations of the body (Clark 1964). The proboscis scalids of *Louisella* are unusual amongst priapulids in being papillate, and by secreting mucus they could have shored up the walls as the animal moved along its burrow. Nothing is known about either the relative depths occupied by various infauna or the maximum depth of burrowing. The abundance of large priapulids would indicate, however, that bioturbation was pronounced (cf. Miller and Byers 1984).

Nektobenthos. Nektobenthic animals are identified on one or more criteria: adaptations consistent with a swimming ability, relative abundance indicating a near-bottom habit within the range of the turbidity flows, and inferred feeding habits inconsistent with an entirely pelagic mode of life. Examples of nektobenthos appear to include the polychaete *Canadia* (Conway Morris 1979c), with large paddle-like neurosetae, and the laterally compressed chordate *Pikaia*. *Eldonia* has been depicted as pelagic (Durham 1974) and, while its abundance at one horizon (Walcott 1911a; Whittington 1971a) could have resulted from the trapping of a shoal, this medusiform echinoderm is

provisionally regarded as nektobenthic. The two species of the swimming arthropod *Perspicaris* are rare, but as they were possibly deposit feeders (Briggs 1977) a pelagic existence presumably can be excluded. *Odaraia* was probably another nektobenthic arthropod (Briggs 1981), while among the miscellaneous category both *Opabinia* (Whittington 1975a) and *Anomalocaris* (Whittington and Briggs 1985) appear to have been well adapted for swimming above the substrate. The pelagic component (Conway Morris 1979a, b, c; Whittington 1981b) apparently includes trilobites (agnostoid and eodiscoid: but see above), and rare soft-bodied animals which may have had a gelatinous composition (*Amiskwia*, *Odontogriphus*), streamlined shape with fins (*Nectocaris*), or prominent natatory organs (*Insollicorypha*, *Sarotrocercus*).

Conclusion. Text-fig. 8 depicts the relative proportions of life habits, excluding pelagic animals which presumably represent an incomplete sample from this ecological zone, in terms of numbers of genera, individuals, and biovolume. The histograms also show the most important group in each category. The general importance of the epifauna is clear, with the vagrant and sessile divisions being dominated by arthropods and sponges respectively. '*Ottoia*' *tenuis* is prominent in the sessile infauna and is inferred to have had a life habit similar to most modern enteropneusts. The vagrant infauna is dominated by priapulids. The important role of the echinoderms in the nektobenthos in terms of individuals and biovolume is due to *Eldonia* (see Durham 1974).

HABITAT



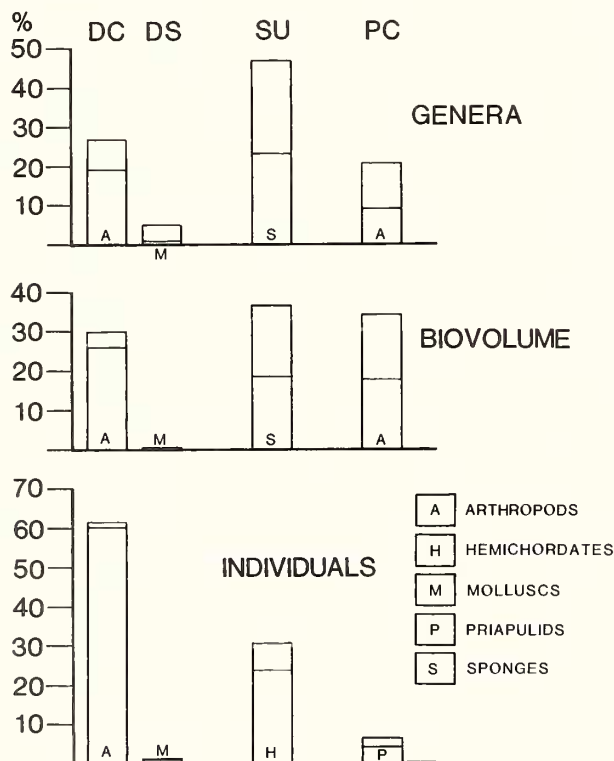
TEXT-FIG. 8. Relative percentages in the Phyllopod Bed (Burgess Shale) of major categories of life habits (NK, nektobenthic; EV, epifaunal vagrant; ES, epifaunal sessile; IV, infaunal vagrant; IS, infaunal sessile) in terms of genera, biovolume, and individuals alive at the time of burial. The most important group within each category is also shown.

Ecology: trophic groups

Introduction. Notwithstanding the soft-part preservation, there are several problems in assessing feeding habits. The extent to which opportunistic feeding (see Cadée 1984) took place is not known and some Phyllopod Bed species may have had catholic diets. It is unfortunate that relatively few species have identifiable gut contents, e.g. hyolithids in *Ottoia*; trilobites, brachiopods, and hyolithids in *Sidneyia*. Accordingly, the structure of the food-collecting apparatus is used as an additional source of evidence. In most cases, therefore, feeding habits are more speculative than life habits and for a substantial fraction of the fauna they remain unknown, a recurrent problem in palaeoecology (e.g. Scott 1978).

Principal feeding categories. The inferred distribution of feeding types with respect to numbers of genera, individuals, and biovolume, and the most important group within each category, is shown in text-fig. 9. Briggs and Whittington (1985) have recently provided a more detailed review of arthropod feeding habits. In text-fig. 9 no distinction is made between high- and low-level suspension feeders, although such information has been presented graphically elsewhere (Conway Morris 1979b). Amongst suspension feeders, sponges predominate in terms of number of genera and biovolume, but the abundance of '*O.*' *tenuis* is reflected in the count of individuals. Deposit (collector) feeders are another important trophic group, with arthropods predominating. Nothing is known of the type of particulate matter (see Johnson 1974) utilized by the various deposit feeders, and such information may not be readily available because of diagenetic alterations. Difficulties in distinguishing scavenging from carnivorous habits in some forms means that they are best taken as a single trophic group. In terms of numbers of genera and individuals this category is not especially notable, but the biovolume of carnivores/scavengers is significant, mostly because of the inclusion of the large

FEEDING HABITS



TEXT-FIG. 9. Relative percentages in the Phyllopod Bed (Burgess Shale) of major trophic categories (DC, deposit, collector; DS, deposit, swallower; SU, suspension; PC, carnivore or scavenger) in terms of genera, biovolume, and individuals alive at the time of burial. The most important group within each category is also shown.

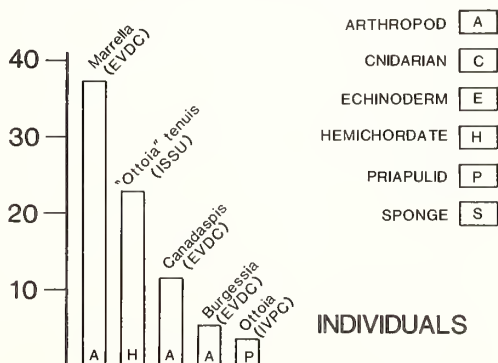
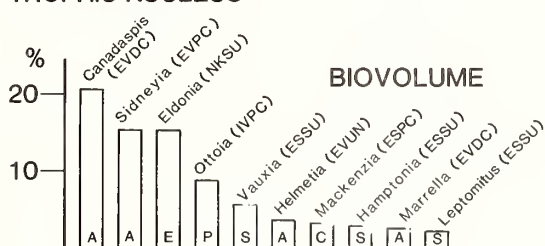
arthropod *Sidneyia* which has gut contents and a feeding apparatus consistent with predatory habits (Bruton 1981). Its importance may have been overestimated because intact exuviae are common and some specimens interpreted as being alive during transport may belong to this category. Nevertheless, *Sidneyia* was probably the most significant predator in the fauna. Together with other carnivorous arthropods (e.g. *Olenoides*, Whittington 1975b; *Naraoia*, Whittington 1977), priapulids (e.g. *Ottoia*, Conway Morris 1977a), and *incertae sedis* such as *Auomalocaris* (Whittington and Briggs 1985), the abundance of *Sidneyia* emphasizes the role of this trophic group in the Phyllopod Bed fauna.

With regard to predation in the Phyllopod Bed community the example of hyolithids in the alimentary tract of *Ottoia* (Conway Morris 1985a) is especially interesting. First, apart from their location, the ingested shells appear to show no evidence of having suffered predation (e.g. scratch marks, crushing), and once returned to the sediment would presumably be indistinguishable from those that perished by more mundane causes. Secondly, a comparison between the number of hyolithids recorded in the guts of *Ottoia* and *Sidneyia*, as against those comprising the free-living standing crop (see sources of data), is indicative of high levels of predation (Conway Morris 1985a). Furthermore, apparent defensive adaptations, such as the spines of *Wiwaxia*, and more circumstantial indications, e.g. frequent breakage of the slender tubes of *Tubulella* into short sections, may be added to the roster of evidence.

Possible evidence for scavenging (in the post-slide environment) by ostracodes on *Marrella* was discussed by Conway Morris (1977a). The relative abundance of this association in the *Marrella* population is very small (c. 0.15%), but the specificity of the ostracodes' location between the median and lateral cephalic spines is so consistent that it may be interpreted better as a symbiotic association formed in the pre-slide environment.

Trophic nucleus. This concept, which is based on Neyman's (1967) criterion of the dominant species that together comprise at least 80% of a fauna's biomass, has been used in a number of palaeo-ecological studies, with the number of individuals necessarily substituting for unavailable data on biomass (e.g. Rhoads *et al.* 1972; Duff 1975; Fürsich 1977; Fürsich and Wendt 1977). Here the

TROPHIC NUCLEUS



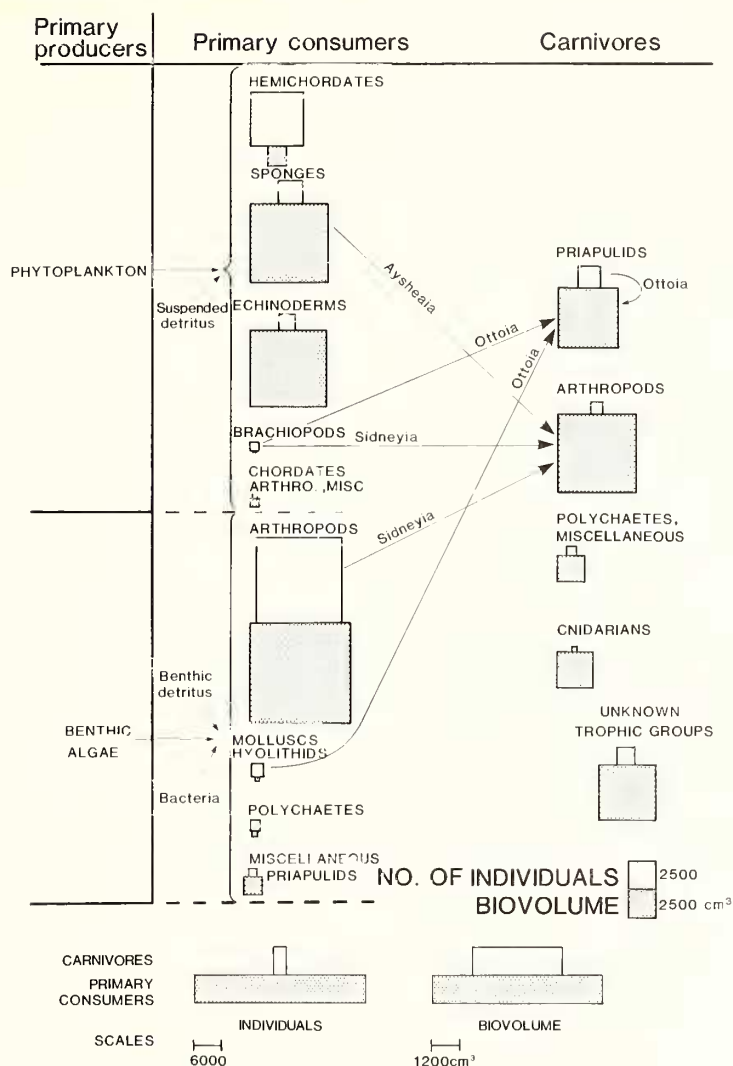
TEXT-FIG. 10. The trophic nucleus of the Phyllopod Bed (Burgess Shale) fauna in terms of biovolume and numbers of individuals alive at the time of burial. Abbreviations for ecological categories given in Table 2.

nucleus is identified both with respect to number of individuals and biovolume, the rank order representing the five and ten most abundant genera respectively within the benthic community (text-fig. 10). The trophic nucleus is more compact when considered in terms of individuals. In each case the dominant species is a deposit (collector) feeding arthropod, but the ranking does not show a close match between the two categories. Thus two of the genera, '*O.*' *tenuis* and *Burgessia*, which rank second and fourth in the trophic nucleus of individuals, have low total biovolumes that exclude them from the latter trophic nucleus. In either case the make up of the trophic nucleus demonstrates that the Phyllopod Bed community was dominated by relatively few species, with *c.* 10% of the benthic species (ranked 1–9 in abundance out of 93) accounting for *c.* 91% of individuals and 82% of biovolume of the entire benthic fauna. This situation is comparable to many modern communities (e.g. Sanders 1960), but direct comparisons between the trophic nucleus of the Phyllopod Bed and 'normal' fossil assemblages is unrealistic because, as Johnson (1964) stressed, the marked dominance of few shelly species in the latter assemblages is likely to be an artefact of preservation rather than a reflection of original biotic proportions.

Turpaeva (1957) drew attention to the widespread, although not invariable, alternation of trophic types in declining species rank within modern benthic communities from the boreal and arctic seas around the USSR; such alternation being linked to division of resources and diminution in feeding competition. Turpaeva's (1957) emphasis on organisms belonging to lower trophic levels, which are often well skeletized (e.g. Schopf 1978; Nicol 1979, 1982), has found considerable palaeontological application (e.g. Rhoads *et al.* 1972; Walker 1972*a, b*; Duff 1975; Fürsich 1977; Fürsich and Wendt 1977; see also Cisne 1973*b*). This analysis follows Duff (1975) in incorporating a wider than usual range of feeding types. In terms of biovolume, no adjacent species within the trophic nucleus share a feeding habit, although the trophic category of *Helmetia* is not known. In terms of individuals, however, the arthropods *Canadaspis* and *Burgessia*, which rank third and fourth in the trophic nucleus, are both interpreted as having the same feeding habit. Whether there was competition for the same resource is debatable. These arthropods differ considerably in size, and the anatomy of their feeding limbs is not especially similar (Hughes 1975; Briggs 1978). It may also be significant that these arthropods appear to show evidence for negative association, in that although both arthropods are very abundant (estimated 2158 specimens of *Burgessia*, 4719 of *Canadaspis* alive at time of burial), co-associations on sawn slabs are rare.

Trophic web. Data on feeding types have been used to reconstruct a tentative trophic web (text-fig. 11), with the importance of major taxonomic groups being assessed in terms of numbers of individuals and biovolume. Direct evidence for primary producers is available from macroscopic benthic algae (Walcott 1919), while G. Wood (pers. comm., 1982) reported an acritarch assemblage dominated by sphaeromorphs and small acanthomorphs. The importance of primary consumers is evident, with suspension feeders presumably capturing phytoplankton and suspended detritus, while deposit feeders are assumed to have exploited bacteria (and other microbial forms), benthic algae, and detritus. A higher trophic level of carnivores is also identified and its significance in the fauna is apparent, especially with respect to biovolume. There is no direct evidence that carnivores occupied more than the primary level, and the apparent absence of secondary or tertiary levels gives the trophic web as reconstructed a relatively simple structure. Establishing whether this simplicity is original is important if meaningful comparisons are eventually to be drawn with trophic webs of younger fossil assemblages and living communities. The restriction of carnivores to a single level and apparent absence of one or a few top carnivores may well be because of incomplete information. Estimates of the efficiency of energy transfer between primary consumers and carnivores are uncertain (see below), but there is no reason to think that relatively inefficient mechanisms of either capture or physiology placed a prohibitive energetic constraint on the existence of top carnivores. More speculatively, appeal could be made to the lower levels of productivity that have been inferred by some authors for the Lower Palaeozoic (e.g. Calef and Bambach 1973) constraining the length of food chains (see also Tappan 1970), and this topic is returned to below.

The few known examples of predatory genera identified in text-fig. 11 serve to emphasize both the



TEXT-FIG. 11. Tentative reconstruction of the trophic web in the Phyllopod Bed (Burgess Shale) community in terms of numbers of individuals alive at the time of burial and biovolume (stippled). Genera known to be carnivores on the basis of gut contents (*Ottoia*, *Sidneyia*) or intimate association with supposed food (*Aysheaia*) are depicted, but must represent only an incomplete part of the transfer of energy to the higher trophic level. Cannibalism has been documented in *Ottoia*. See text for further discussion.

scarcity of data and a resulting inability to reconstruct this web in more detail. Evidence for predation by *Ottoia*, which appears also to have been cannibalistic (Conway Morris 1977a), and *Sidneyia* was alluded to above. Frequent association between *Aysheaia* and several species of sponge suggests that it fed on these organisms. Comparison between individuals and biovolume totals of primary consumers (deposit and suspension feeders taken together, see Stanton and Nelson 1980; cf. Scott 1972; Fürsich and Wendt 1977) and carnivores allows approximate estimates of the degree of

energetic efficiency operating between these two trophic levels: in terms of individuals the percentage of predators in comparison with deposit and suspension feeders is *c.* 7%, while for biovolume the equivalent value is much higher at 52%. The lower value is comparable to some other estimates of the efficiency in energy flow between marine trophic levels (*c.* 10–12%; Stanton and Nelson 1980; see also Powell and Stanton 1985), but it is based on individuals with wide size ranges and, by implication, calorific values. The presumably closer relationship between biovolume and original biomass might suggest that the value of 52% is slightly more accurate, assuming that biomass of all species is proportional to the same energetic equivalents. The tenuous connection between biovolume and biomass, however, together with problems in calculating accurately biovolume of a population and questionable assumptions, such as the apparent absence of second (and third) levels of carnivores, suggests that this higher figure is an overestimate.

Given the problems inherent in palaeoecology it is not surprising that relatively few workers (e.g. Kapp 1975; Fürsich and Wendt 1977; Stanton and Nelson 1980) have attempted to reconstruct the trophic web of a given marine fossil assemblage. Text-fig. 11 depicts what is the most complete trophic reconstruction so far compiled for a Lower Palaeozoic marine community, yet it is sobering to consider that, despite extensive soft-part preservation, neither a detailed reconstruction of the trophic web with reliable indications of feeding habits of individual species, nor a well-constrained estimate of the efficiency of energetic transfer is available for the Phyllopod Bed community.

The relative importance of combinations of life habit and feeding type with respect to numbers of genera and individuals and biovolume (Table 3) shows that, in terms of number of individuals, ecological category EVDC (epifaunal, vagrant, deposit (collector) feeder; see Table 2) is the most important, with ISSU (infaunal, sessile, suspension feeder) rating a low second. With regard to biovolume, EVDC is again significant, but other notable categories include NKSU (nektobenthic,

TABLE 3. Relative importance of various ecological categories in the Phyllopod Bed fauna (see Table 2 for explanation of abbreviations). Pelagic and benthic components are treated separately. Excluded combinations include PSDC, PSDS, PFDC, and PFDS; unknown but theoretically possible combinations include NKDC, NKDS, EVSU, ESDC, ESDS, IVSU, ISDS, and ISPC.

Ecological category	Number of genera	Per cent individuals	Per cent biovolume
Pelagic: PSSU	2	80.00	39.70
PSPC	2	13.30	6.40
PFSU	1	6.70	53.90
Benthic: NKSU	3	2.08	15.34
NKPC	3	0.56	1.81
NKUN	1	0.06	0.02
EVDC	17	59.06	26.87
EVDS	3	1.05	0.05
EVPC	8	1.32	16.39
EVUN	10	0.96	6.43
ESSU ^H	24	3.87	16.81
ESSU ^L	9	0.73	0.03
ESPC	1	0.22	3.30
ESUN	1	< 0.01	< 0.01
IVDC	3	0.19	0.22
IVDS	1	0.03	< 0.01
IVPC	4	4.45	10.00
IVUN	2	0.04	0.27
ISDC	1	0.94	0.08
ISSU	1	23.01	1.04
UNUN	1	1.42	1.34

suspension feeder), EVPC (epifaunal, vagrant, carnivore/scavenger), ESSU^H (epifaunal, sessile, high level suspension feeder), and IVPC (infaunal, vagrant, carnivore/scavenger).

Dominance diversity and possible niche partitioning

Introduction. Dominance–diversity curves were prepared for a number of ecological categories in the Phyllopod Bed fauna. Such curves have found wide ecological application (e.g. Whittaker 1965, 1972, 1975; May 1975, 1981) and, despite problems of time-averaging and preservation bias in fossil assemblages, this technique has been employed on occasion by palaeontologists (e.g. McBride 1976; Schwartz *et al.* 1977; McGhee 1981) and in sub-fossil assemblages by palaeolimnologists (e.g. Goulden 1966, 1969; Deevy 1969; but see Smol 1981), while Driscoll and Swanson (1973) considered potential palaeontological applications with particular regard to epifaunal assemblages. Much of the interest in dominance–diversity curves has been concerned with their depiction of resource subdivision and so their possible use as indicators of niche partitioning. Three principal distributions have been noted; particularly useful discussions regarding them have been provided by Whittaker (1972) and May (1975). Two of the distributions relate to models that describe resource appropriation in terms of ‘random niche boundaries’ (often referred to as the broken-stick model; not considered further here, see below) and ‘niche pre-emption’. The third, the log-normal distribution, traditionally has been interpreted as a mathematical artefact arising from the Central Limit Theorem and resulting from the interaction of many more or less independent factors that reflect a wide number of variables, most typically involving a large number of species with little resource overlap. More recently, however, biological explanations of a log-normal distribution have been offered. Sugihara (1980) proposed that this distribution was a consequence of the segmental division of niche space in a hierarchically structured community, while Ugland and Gray (1982; see also Shaw *et al.* 1983) proposed an alternative explanation and linked log-normality with community equilibrium. A geometric distribution is usually linked to the niche pre-emption model, in which the dominant species takes a given fraction (k) of a resource, the next dominant species a fraction (k) of the remainder of the resource, and so on.

Results. The dominance–diversity curves for four simple ecological categories (IVPC, EVPC, EVDC, and ESSU^H; see Table 2), all epifaunal vagrant animals (EV/DC + DS + PC + UN), and the entire benthic fauna (i.e. excluding PS + PF), are depicted in text-fig. 12, while the relevant statistics are given in Table 4. Each graph was prepared in the standard manner by plotting the abundance, in this case according to both numbers of individuals and total biovolume, against the rank abundance (1– n , most to least abundant). Visual inspection of the curves is liable to be misleading, and they were analyzed statistically for goodness-of-fit (square correlation, r^2) for each of the three principal distributions mentioned above (Table 4). These statistics and calculations of diversity (the widely used Shannon–Wiener index $H' = - \sum_{i=1}^n p_i \log_2 p_i$, where p_i is the proportion of the i th species) and evenness ($\epsilon = H'/\log S$, where S is the total number of species) were kindly computed by J. J. Sepkoski (University of Chicago). The test statistics also allowed the possibility of further sampling by the hypothetical addition of ‘undiscovered’ species. This is the equivalent procedure to drawing the ‘veil-line’ of a log-normal distribution to the right to reveal rarer species (Preston 1962). The large samples from the Phyllopod Bed suggests that the differences between the observed and original diversity may have been relatively small, and that the hypothetical addition of a large number of undiscovered species to each category may be unwarranted.

In no case did the broken-stick (random niche boundary) model provide a good fit to the dominance–diversity data. In the majority of cases the distribution in terms of both numbers of individuals and biovolumes was best explained by a log-normal distribution (text-fig. 12; Table 4). In the case of the larger categories of all epifaunal vagrant animals and the entire benthic fauna such a distribution may well be an artefact reflecting their heterogeneous ecological composition, but for smaller categories the alternative biological explanations of Sugihara (1980) and Ugland and Gray (1982), in principle, are feasible. In a few cases a geometric distribution provided the best-fit, and

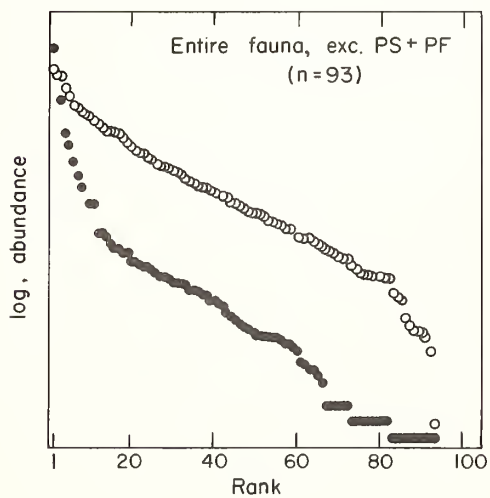
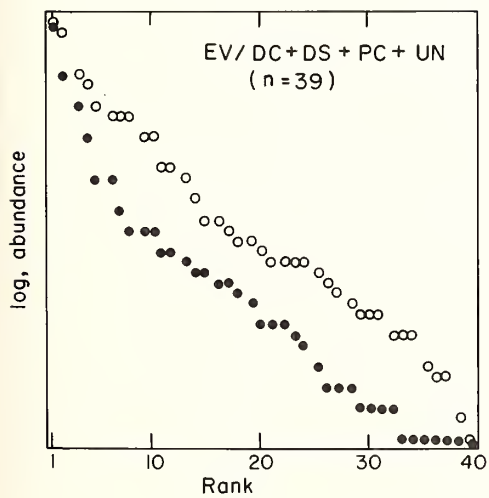
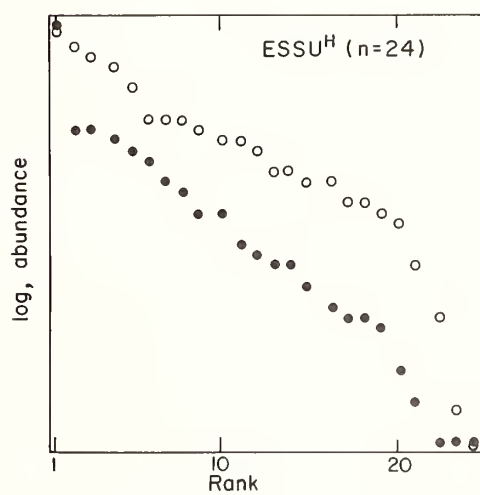
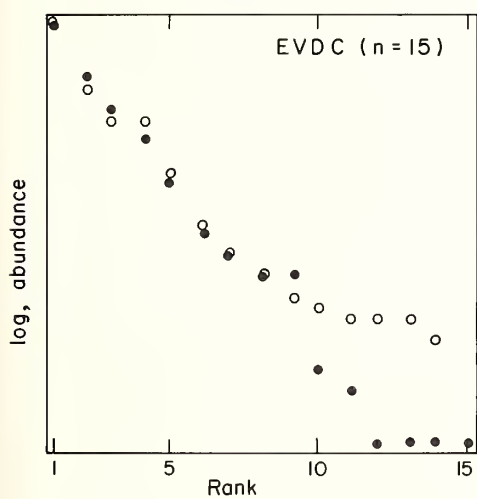
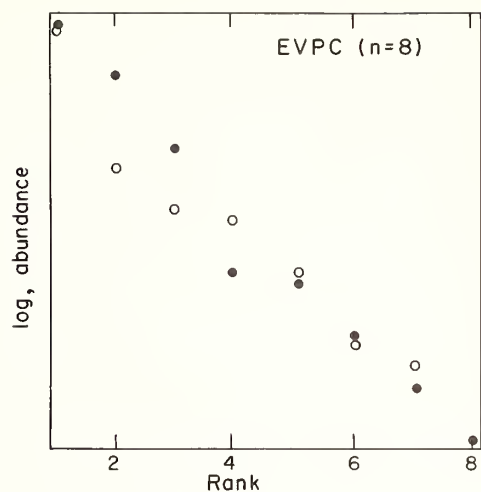
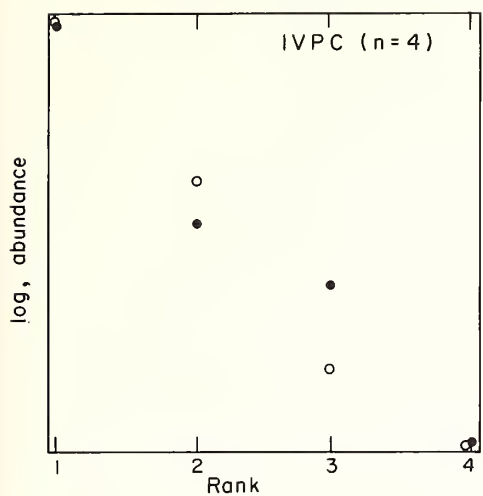
TABLE 4. Distribution (log-normal or geometric) that best explains dominance–diversity curves in seven ecological categories or portions of the Phyllopod Bed (Burgess Shale), with calculated goodness of fit. Where hypothetical addition (up to six) of taxa alters the distribution, this is indicated. The geometric distribution remains unaltered if further taxa are added. Values of diversity (Shannon–Wiener H') and evenness (ϵ) are also given for each category or portion (see text for further details).

Category	Individuals	Biovolume
IVPC	Log-normal (0.9791) $H' = 0.587$, $\epsilon = 0.424$	Geometric (0.9698)
		+2 Log-normal (0.9808)
		+4 Log-normal (0.9834)
		$H' = 0.405$, $\epsilon = 0.292$
EVPC	Geometric (0.9711) +2 Log-normal (0.9776) +6 Log-normal (0.9763) $H' = 1.767$, $\epsilon = 0.850$	Log-normal (0.9620)
		$H' = 0.287$, $\epsilon = 0.138$
EVDC	Geometric (0.9669) $H' = 1.103$, $\epsilon = 0.407$	Log-normal (0.9397)
		$H' = 0.764$, $\epsilon = 0.282$
ESSU ^H	Log-normal (0.9765) +6 Geometric (0.9673) $H' = 2.149$, $\epsilon = 0.676$	Log-normal (0.9058)
		+6 Geometric (0.8581)
		$H' = 1.982$, $\epsilon = 0.624$
EV/DC + DS + PC + UN	Log-normal (0.9378) $H' = 1.343$, $\epsilon = 0.367$	Log-normal (0.9873)
		$H' = 1.675$, $\epsilon = 0.457$
Entire fauna, excluding PS + PF	Log-normal (0.9549) $H' = 2.094$, $\epsilon = 0.462$	Log-normal (0.9891)
		$H' = 2.624$, $\epsilon = 0.579$
Fauna, hard parts	Geometric (0.9144) $H' = 1.843$, $\epsilon = 0.699$	Log-normal (0.8743)
		$H' = 0.635$, $\epsilon = 0.240$

therefore might conceivably reflect niche pre-emption (Table 4). In categories IVPC (biovolume) and EVPC (individuals), however, hypothetical addition of species resulted in the distribution being better explained by log-normality. Conversely, further hypothetical sampling in category ESSU^H (individuals and biovolumes) resulted in a geometric distribution providing a better fit than a log-normal distribution. Finally, in category EVDC (individuals) a geometric distribution was maintained in the face of further sampling. The dominance–diversity data for those elements of the fauna with hard parts (excluding sponges, but including rare benthic echinoderms) that were alive at the time of burial were also assessed (Table 4), as this distribution is relevant to that portion of the standing crop that would be expected to fossilize and provide a ‘typical’ assemblage (see also Lasker 1976). The figures are based on major assumptions (see sources of data), and a geometric distribution providing the best fit in terms of individuals is unlikely to be of any biological significance.

Conclusion. These results broadly accord with a more extensive survey of dominance–diversity in fossil assemblages by Schwartz *et al.* (1977), who noted the predominance of log-normal distributions. Nevertheless, it seems possible that in at least ecological category EVDC partitioning resources followed the niche pre-emption model. In a study of Upper Cambrian communities McBride (1976) portrayed dominance–diversity curves of polymeroid trilobites, reconstructed as

TEXT-FIG. 12. Dominance–diversity curves for four ecological categories (IVPC, EVPC, EVDC, ESSU^H) and two major portions (EV/DC + DS + PC + UN; entire benthic fauna, excluding PS + PF) of the Phyllopod Bed (Burgess Shale) fauna in terms of individuals alive at the time of burial (filled circles) and biovolume (open circles). See Table 2 for explanation of abbreviations; see Table 4 for preferred distribution (log-normal or geometric), goodness of fit (r^2), diversity (H'), and equitability (ϵ).



epifaunal vagrant deposit feeders, and interpreted his data as probably reflecting niche pre-emption. Re-analysis of his data, however, does not support a geometric distribution (J. J. Sepkoski, pers. comm.), although McBride's (1976, p. 147) comments on the likelihood of severe competition and niche partitioning amongst deposit feeders may still hold.

COMPARISONS BETWEEN THE PHYLLOPOD BED AND OTHER COMMUNITIES

Cambrian communities

Introduction. The ecological data from the Phyllopod Bed fauna provide a unique insight into the structure of a relatively deep-water Cambrian community. Useful comparisons with other Cambrian assemblages are dependent on the observation that, had the Phyllopod Bed fauna failed to experience those conditions conducive for soft-part preservation, then (as noted above) the impoverished shelly fauna would be indistinguishable in general taxonomic outline from most other Cambrian assemblages. The minor role of shelly taxa in the ecological spectrum of the Phyllopod Bed, especially with respect to numbers of individuals, means that synecological pronouncements based on 'typical' Cambrian faunas are likely to be insecure. Detailed comparisons with other fossil assemblages of Cambrian age are not straightforward however, both on account of a general absence of soft-bodied forms and the inhabited range of marine environments.

Ecological comparisons. On the basis of shelly faunas, Cambrian marine life has been characterized as ecologically generalized, with broad niches and a relatively simple trophic structure dominated by detritus and low-level suspension feeders. In general, such communities are identified as having wide environmental tolerances that are reflected in broad distributions and diffuse boundaries (e.g. Valentine 1973; Sepkoski 1979; Sepkoski and Sheehan 1983). Information on the overall distribution of the Phyllopod Bed fauna and its relative distinctiveness in comparison with other benthic communities in the off-reef Stephen Formation is difficult to assess on present evidence, although the recurrent nature of a Raymond Quarry-like biota is some evidence for community identity (Collins *et al.* 1983). Ecologically, however, the Phyllopod Bed community does not entirely correspond with the characterization of Cambrian life as based on the shelly component. It is indeed true that detritus and suspension feeders predominate (text-figs. 9–11), but the possibility of niche partitioning in at least one group of deposit feeders (text-fig. 12; Table 4) may point to a hitherto unsuspected ecological complexity. With regard to epifaunal suspension feeders, their distribution and history of tiering is reviewed by Ausich and Bottjer (1982). The existence in the Phyllopod Bed of a low level with mostly brachiopods and rare edrioasteroids, and higher levels dominated by sponges together with much rarer pelmatozoan echinoderms (eocrinoids and primitive ?crinoids) corresponds well with Ausich and Bottjer's (1982) descriptions, but the maximum height above the substrate may have been twice as high (20 cm) as they reported (see Conway Morris 1979b).

In terms of trophic analysis, however, nowhere is the contrast between the Phyllopod Bed fauna and other Cambrian assemblages more apparent than on the role of predation (text-figs. 9 and 11). The presence of a significant proportion of predators in the Phyllopod Bed suggests that trophic descriptions of other Cambrian communities have been biased severely by fossilization potential. On the basis of shelly faunas, macrophagous predators have been inferred to be either rare or even absent, especially in the Lower Cambrian (e.g. Glaessner 1972; Valentine 1973, 1975). In one of the very few Cambrian community studies, McBride's (1976) analysis of open shelf and 'shoaling' shelf biofacies in the Upper Cambrian *Dunderbergia* Zone of western USA, which was based on shelly faunas, made no mention of carnivores or scavengers. Bambach (1983) claimed in his synthesis of marine guilds and ecologies through geological time that Cambrian faunas have few carnivores, most of which were referred to vaguely as infaunal 'polychaetes' (his fig. 3). Hutchinson (1961; see also Matthew 1891; Bengtson 1977) perceptively suggested, however, that the absence of Cambrian predators may be an artefact arising from their having a minimal fossilization potential, a trait that continues into present-day marine communities (Schopf 1978; Nicol 1982). The abundance of effectively soft-bodied

carnivores in the Phyllopod Bed combined with various other lines of evidence (Conway Morris 1985a; Conway Morris and Jenkins 1985) amply confirms Hutchinson's insights. Even apparent carnivores with hard parts, such as the trilobite *Olenoides* (Whittington 1975b, 1980b), would not be readily attributable to this trophic group in the absence of exceptional preservation. This is because, paradoxically, the feeding appendages have a minimal preservation potential, and the exoskeleton is unlikely to provide direct evidence on the style of feeding.

Regarding the other major ecological category discussed above, that of life habits (Table 2), direct comparisons between their relative proportions in the Phyllopod Bed (text-fig. 8) and other Cambrian communities are not straightforward, both because of severe taphonomic bias in 'normal' shelly faunas and a lack of published studies. One instance where a comparison may have some validity is in the slightly younger Wheeler Formation of Utah, where the frequency distribution of the principal shelly groups is statistically similar to the equivalent component from the Burgess Shale (Conway Morris and Robison 1982). From one prolifically fossiliferous horizon in the House Range, which has yielded some exceptionally preserved material, Robison (1985) commented on the absence of an infauna and the predominance of a vagrant epifauna. In the overlying Marjum Formation Rogers (1984) speculated on the likelihood of some communities being dominated by epifaunal sponges. In a broader survey of Upper Cambrian communities McBride (1976) portrayed a far less diverse range of life habits, although in this instance taphonomic factors must be a source of severe bias.

Younger Palaeozoic communities

Introduction. Taxonomic differences aside, it may transpire that the community structure of the Phyllopod Bed fauna was not fundamentally different from that of many younger Palaeozoic soft-bottom faunas (see also Bretsky 1969) in that patterns of resource supply and distribution presumably did not change radically until at least the late Silurian, when the introduction of abundant terrestrial plant debris may have influenced community structure (Bambach 1977; see also Calef and Bambach 1973). Calef and Bambach (1973) argued that in the absence of a pre-Silurian terrestrial flora and its associated influence on rates of chemical weathering, nutrient supply into the shallow seas was drastically diminished while 'Deep basin benthos was generally excluded for lack of food'. While nutrient supply may have been lower during the early Palaeozoic, the diversity and abundance (reflecting biomass) of Phyllopod Bed organisms casts some doubt on Calef and Bambach's (1973) general thesis. Moreover, deep-water Cambrian (Hales Limestone) faunas, possibly living in excess of 1600 m (Cook and Taylor 1977), also demonstrate that a deep basin benthos was present and very widespread. Admittedly the trilobite faunas are not diverse (Taylor 1976; Taylor and Cook 1976) and the scarcity of burrowing (Taylor and Cook 1976; Cook and Taylor 1977) indicates a restricted infauna, but the abundance of sponge spicules suggests the former presence of suspension feeders, a mode of life that is energetically marginal (Jørgensen 1966). Discussion of nutrient levels in Cambrian oceans and their comparison with younger systems is perhaps more one of degree than kind. Palaeo-oceanographic factors must have been significant, and productivity of the Phyllopod Bed fauna, for example, may have been favoured by proximity to the reef and more generally seasonal (winter) upwelling (see Parrish 1982, fig. 5).

Evolution of ecological categories. Various attempts have been made to study trophic replacement in marine communities through geological time (e.g. Ager 1976; McGhee 1981). The tracing of ecological analogues of deeper-water Cambrian communities, as typified by the Phyllopod Bed fauna, through time is complicated by specialization (niche partitioning) and associated proliferation of taxa, especially in the Ordovician, and the longer-term decline of major groups and the rise of others. At least two approaches, however, hold some promise. First, there have been repeated suggestions that oxygen levels in early Palaeozoic oceans were considerably less than those of the present-day. With particular reference to the Phyllopod Bed community, there is evidence to suggest that it was adjacent to anoxic water and, given such proximity, may itself have been within a dysaerobic zone (see Rhoads and Morse 1971). In describing metazoan faunas from a Canadian fjord subject to low oxygen levels, Tunnicliffe (1981) suggested that they might provide a useful analogue to

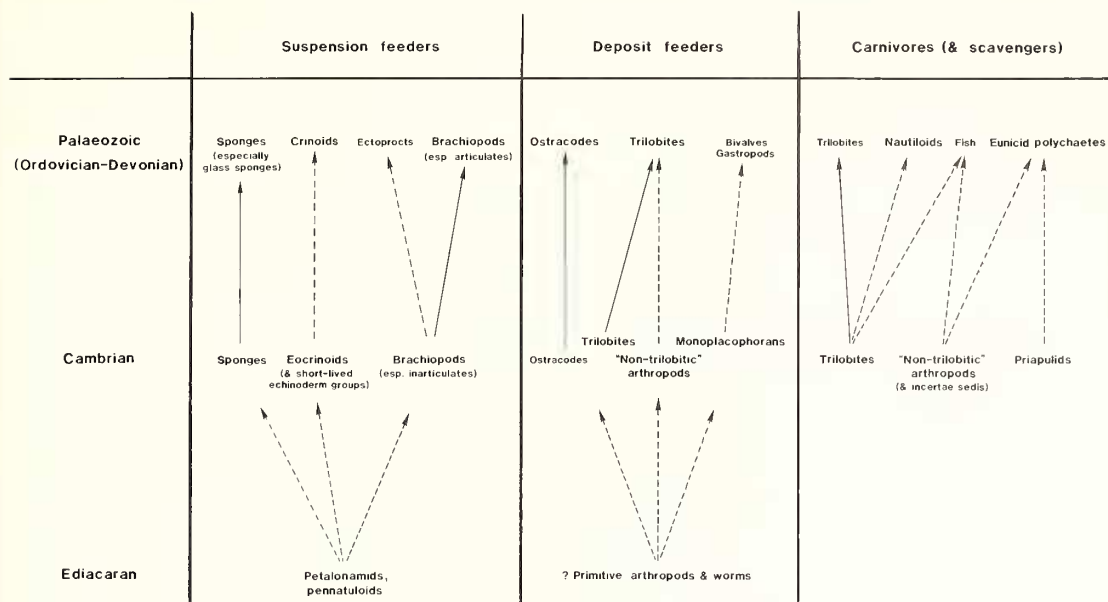
early Palaeozoic faunas. Evidence of at least episodic states of low oxygenation in early Palaeozoic oceans is known (Leggett *et al.* 1981) and a specific study through time of metazoan communities inhabiting poorly oxygenated environments, for which various criteria exist (see Savrda *et al.* 1984), may prove fruitful. Byers (1979) has provided initial pointers in his study of the ichno-faunas of dysaerobic basins through geological time, and Savrda *et al.* (1984) have reviewed critically some applications arising from this and related work. How effectively such ecological analogues can be pursued through geological time, however, is not yet clear.

Irrespective of similarities or differences in biotic and ecological composition, it is, of course, no coincidence that the likelihood of soft-part preservation would be greatly enhanced in such dysaerobic-anoxic environments, especially given the prevalence of fine-grained sediment accumulation and opportunities for catastrophic burial, such as that provided by sediment put into suspension by storms or turbidity currents.

A more general method of tracing ecological analogues lies in an examination of deeper-water faunas through geological time. It has been claimed that there is an off-shore displacement of benthic communities, corresponding to the three great 'evolutionary faunas' of the Phanerozoic (Cambrian, Palaeozoic, Modern) through time, with the relatively archaic 'Cambrian fauna' migrating into deeper-water during post-Cambrian times (Jablonski *et al.* 1983; Sepkoski and Sheehan 1983; see also Axelrod 1958; Berry 1972; Rowland *et al.* 1984). According to this hypothesis, younger equivalents to the Phyllopod Bed community may be best sought in deeper-water facies (but see Bretsky and Klofak 1985). Of the relevant Upper Cambrian and Ordovician communities from North America listed by Sepkoski and Sheehan (1983), only Beecher's Trilobite Bed in the Frankfort Shale (Caradoc) shows soft-part preservation (Cisne 1973*b*, 1981). Elsewhere diversity information is limited to shelly species, so comparisons are not straightforward.

The following attempt to document the broadest patterns of ecological replacement in deeper-water faunas is based on the simple trophic groups of deposit feeders, suspension feeders, and carnivores. In Beecher's Trilobite Bed deposit feeders appear to have included trilobites and ostracodes, and these two groups figure prominently in the almost coeval *Triarthrus* community of the Trenton Group (Titus and Cameron 1976). Trilobites, and more especially ostracodes, may represent the ecological descendants of the extraordinarily diverse arthropod fauna, dominated by deposit feeders (text-fig. 9), of the Phyllopod Bed. This transition may have occurred by the Upper Cambrian in that at least some relatively deep-water sediments (Orsten) had a diverse micro-arthropod fauna, including ostracodes and small crustaceans (e.g. Müller 1979, 1981, 1982, 1983, 1985). However, as Müller stressed, much of the contrast between these Upper Cambrian arthropod faunas and those of the Burgess Shale could be a result of different modes of preservation, with selective phosphatization of small fossils in the Upper Cambrian Orsten. The phylogenetic relationships between these Middle and Upper Cambrian arthropods are obscure (Müller 1983), and it is therefore the more interesting to note a further example of apparent ecological continuity between the marrellomorph arthropod *Mimetaster* from the Lower Devonian Hunsrückschiefer (Birenheide 1971; Stürmer and Bergström 1976) and the apparently related Phyllopod Bed *Marrella* (Whittington 1971*b*). Other deposit feeders, at least locally, were the molluscs. In the Cambrian these were predominantly monoplacophorans, while in some younger communities (especially Silurian) ecological descendants may have included infaunal bivalves with rare gastropods (and monoplacophorans) also ecologically replacing in part the trilobites (e.g. Hurst and Watkins 1981).

Turning to low-level suspension feeders in deep-water Ordovician facies, the brachiopods were presumably little different ecologically from those of the Phyllopod Bed and include both inarticulates and articulates. High-level suspension feeders include pelmatozoan echinoderms (especially crinoids), locally dendroid graptolites and sponges, but the latter group may be under-represented by methodological oversight and taphonomic factors. Taylor and Cook (1976; Cook and Taylor 1977) noted an abundance of sponge spicules in deep-water Upper Cambrian deposits, and other comparisons between these deep-water faunas and the Burgess Shale were drawn above. Examples of exceptional preservation, such as the celebrated deep-water sponges from the late Devonian of the Appalachians (Hall and Clarke 1900; Clarke 1918; Caster 1939) probably reflect the



TEXT-FIG. 13. Simplified diagram showing possible descent of ecological analogues of suspension feeders, deposit feeders, and carnivores in the early Phanerozoic deeper-water communities; see text for sources of data and further discussion. Solid arrows indicate descent within the same group, although not necessarily with direct phylogenetic links; dotted arrows indicate an indirect relationship. Size of lettering indicates relative importance.

spread of cold-water conditions (McGhee 1982), but similar sponge faunas may formerly have been widespread in deep-water communities with a low preservation potential.

The ecological equivalents of the epifaunal predators of the Phyllopod Bed are less easily identifiable but may include fish, nautiloids, and perhaps some trilobites. No unequivocal analogue to the infaunal priapulid predators of the Phyllopod Bed appears to have been recognized but, if jawed polychaetes represent their ecological descendants (Conway Morris 1977a), dispersed scolecodonts should occur in these later deep-water facies.

Text-fig. 13 summarizes in a highly simplified fashion the proposed evolution of ecological analogues in deeper-water communities from the Cambrian to the Devonian. In some cases ecological descent is linked to phylogenetic descent, but more often the successors are not closely related to the earlier forms. The ecological replacements depicted here may have arisen by either opportunistic or competitive displacement. This diagram is tentative, but differs somewhat from earlier depictions of Palaeozoic marine community evolution (e.g. Bretsky 1969; Berry 1974; Hurst and Watkins 1981; Lockley 1983) in emphasizing the more synecological aspects, albeit at a simplified level, and by drawing on information from soft-bodied Lagerstätten (Burgess Shale, Beecher's Trilobite Bed (Cisne 1973a, b), Hunsrückschiefer (Stürmer *et al.* 1980)). More effective comparisons of deep-water ecologies during the Palaeozoic will be enhanced by as yet unavailable community studies of appropriate Lagerstätten.

Concluding remarks. If the assumption that the origins of the 'Cambrian fauna' ultimately lay in very shallow water (Axelrod 1958; Sepkoski and Sheehan 1983) has any validity, then extrapolation of Phyllopod Bed (Burgess Shale) ecological equivalents to older faunas presumably should concentrate on shallow-water assemblages of earliest Cambrian (Tommotian) or even Ediacaran age (text-fig. 13). Ecological comparisons are hindered by major environmental differences, e.g. turbulence, oxygen, substrates, and possibly salinity. Nevertheless, it may be significant that shallow-

water Tommotian faunas contain abundant halkieriids, known from their dispersed sclerites, descendants of which occur in the deeper-water Phyllopod Bed (Bengtson and Conway Morris 1984; Conway Morris 1985a).

In addition, an indication of the ecologies of the pre-skeletal Ediacaran fauna, some of which were apparently deep-water, is given (text-fig. 13). These faunas were apparently dominated by suspension feeders, which in the case of cnidarians conceivably were microcarnivores on protoctistans, metazoan larvae, and other plankton. Deposit feeders and perhaps grazers were evidently represented by worms such as *Dickinsonia* (Wade 1972), the primitive ?arthropods, and probably some of the makers of the abundant trace fossils. Macrophagous predators and scavengers appear to have been absent (Glaessner 1984).

Apparently only one reconstruction of a feeding web for an Ediacaran assemblage has been attempted (Goldring 1972), and this makes possibly unwarranted assumptions regarding the presence of predatory groups (as nemerteans). The available evidence points to a simple trophic structure in Ediacaran communities. The inference that microbial decomposers to some extent usurped the role of higher trophic levels, however, may be difficult to reconcile with the widespread survival of soft parts.

Recent communities

Modern dysaerobic communities do not appear to have a Palaeozoic aspect (Savrda *et al.* 1984; Thompson *et al.* 1985), but it may be significant that, as reconstructed, the Phyllopod Bed fauna has a number of functional and ecological similarities with modern deep-sea faunas. Moreover, a number of authors (e.g. Hickman 1981; Thayer 1983) have commented on ecological (not usually phylogenetic) similarities between Palaeozoic faunas and modern assemblages living in the deep sea as well as shallower waters around Antarctica. More specifically I wish to stress that detailed ecological investigations of certain modern refugia (for a recent discussion see Thayer 1983) may enhance our understanding of the make-up of ancient communities by way of analogy. For example, modern deep-water ahermatypic mounds may include substantial numbers of articulate brachiopods and stalked crinoids, an assemblage with a remarkably Palaeozoic aspect (Heckel 1974) that if transferred to shallow (and readily accessible) waters probably would be hailed as an outstanding relic.

Concluding observations

The preceding attempt to trace ecological analogues in relatively deep-water faunas through geological time may be widened to a more general documentation of increasing ecological complexity during the early metazoan radiations. This topic has already received attention from studies of changing trace fossil diversities (e.g. Alpert 1977; Brasier 1979), tiering of sessile epifauna and infauna (Ausich and Bottjer 1982), and specific groups such as echinoderms (Sprinkle 1980). The contrasts between the ecology of Ediacaran and Cambrian (e.g. Phyllopod Bed) communities are striking and text-fig. 13 serves to stress the radical innovations that must have accompanied the appearance of numerous bodyplans. The appearance of carnivores which evidently occurred in the Lower Cambrian (see Conway Morris 1985a; Conway Morris and Jenkins 1985) is the most obvious trophic innovation, and has a direct bearing on the long standing debate on whether hard parts evolved as a protective adaptation. Niche differentiation in suspension feeders included tiering (Conway Morris 1979b; Ausich and Bottjer 1982), and possibly different size/type selection of food particles amongst the various tentacular and sieve organs of established and newly evolving bodyplans. Amongst deposit feeders, the possibility of niche pre-emption in one ecological category (EVDC, epifaunal, vagrant, deposit (collector) feeder) of the Phyllopod Bed fauna may indicate that these resources were apportioned.

It remains to be seen whether niche differentiation proceeded at different rates in different ecological categories (see also Bambach 1983). Styles of deposit feeding may have shown no radical change for hundreds of millions of years (Levinton and Bambach 1975), but amongst suspension feeders the development of tiering and increased vertical range is indicative of continuing specialization (Ausich and Bottjer 1982). In the case of predation, although the existence of

Cambrian predators is now firmly established, it seems plausible that the degree of sophistication in styles of predation (search and attack) and deterrence in comparison with younger Palaeozoic faunas (Signor and Brett 1984) was substantially less.

The mode and tempo by which the 'ecological barrel' was filled will be understood better when Lower Cambrian communities, including those of soft-bodied Lagerstätten such as the Kinzers Formation (Pennsylvania), are better documented. Preparation of dominance-diversity curves through geological time (see McGhee 1981 for preliminary analysis of changes in off-shore and near-shore communities during a 5 Ma span (Frasnian, Devonian)) may provide further insights into ecological diversification of both entire communities and particular ecological categories. Analogies may exist with some patterns documented in short-term ecological successions (e.g. Whittaker 1972; Bazzaz 1975; see also Kempton and Taylor 1976). Conceivably the earliest stages in the filling of the Phanerozoic 'ecological barrel' may have entailed minimal competition in marine environments (Conway Morris and Fritz 1984), and niche structure may show a non-overlapping and non-contiguous nature.

THE ROLE OF FOSSIL LAGERSTÄTTEN

The frequency of fossil Lagerstätten

The Phyllopod Bed fauna provides such a wealth of insights into the ecology and diversity of Middle Cambrian life that it is appropriate to inquire whether similar soft-bodied Lagerstätten occur with sufficient frequency during the Phanerozoic to provide ultimately a more comprehensive view of the palaeoecology and community structure of former life. As Table 5 demonstrates the Phyllopod Bed is indeed only one of many exceptional deposits, but this list is based on a number of important qualifications. Only the four most diverse Ediacaran faunas from the Late Precambrian are included, although there are numerous other localities (e.g. Canada (Northwest Territories and British Columbia), China, England, Wales, Iran, Morocco, Siberia, Sweden, Ukraine, USA (North and South Carolina)) where certain elements of the Ediacaran biota have been found. The widespread occurrence of the entirely soft-bodied Ediacaran fossils is linked to an apparent absence of scavengers and predators combined with a restricted degree of burrowing and other bioturbation; such conditions favour extensive soft-part preservation (Sepkoski 1979; Glaessner 1984). With the

TABLE 5. List of principal Lagerstätten with soft-part preservation, excluding pre-Ediacaran examples (e.g. Gunflint Chert).

Deposit	Age	Locality	Environment of deposition
Permafrost, frozen mammoths and other mammals	Pleistocene	Siberia, USSR	Tundra
Calico Mountains nodules (Barstow Formation)	Miocene	California, USA	Fluvial, lacustrine
Monterey Formation	Miocene	California, USA	Marine
Oeningen Molasse	Miocene	Lake Constance, Switzerland/Germany	Lacustrine, fluvial
Amber	Oligocene	Baltic region, Dominican Republic	Terrestrial
Florissant Beds	Oligocene	Colorado, USA	Lacustrine
Quercy Phosphorites	Eocene-Oligocene	Massif Central, France	Terrestrial
Geiseltal Lignite	Eocene	Halle, East Germany	Terrestrial, swamp
Messel Oil Shales	Eocene	Darmstadt, West Germany	Lacustrine
Monte Bolca Fish Beds	Eocene	Monte Bolca, Italy	Marine
Green River Formation	Eocene	Wyoming, Utah, Colorado, USA	Lacustrine
Sahel Alma Fish Beds	Cretaceous	Lebanon	Marine

TABLE 5 (*cont.*)

Deposit	Age	Locality	Environment of deposition
Amber	Cretaceous	Lebanon, Canada	Terrestrial
Solnhofen Limestone	Jurassic	Bavaria, West Germany	Marine
Cerin Limestone	Jurassic	Jura, France	Marine
Posidonia Shale (Holzmaden)	Jurassic	Württemberg, West Germany	Marine
Selcifero Lombardo	Jurassic	Osteno, Italy	Marine
Voltzia Sandstone	Triassic	Northern Vosges, France	Marine, deltaic
Mecca and Logan Black Shales	Carboniferous	Indiana, USA	Marine
Mazon Creek nodules	Carboniferous	Illinois, USA	Terrestrial/marine
Montceau-les-Mines concretions and shales	Carboniferous	Autun, France	Terrestrial/marine
Granton Sandstones	Carboniferous	Granton, Scotland	Marine
Bear Gulch Limestone	Carboniferous	Montana, USA	Marine
Bearsden (Top Hsie Limestone)	Carboniferous	Glasgow, Scotland	Marine
Gilboa mudstones	Devonian	New York, USA	Terrestrial
Hunsrück Slate	Devonian	Rhineland, West Germany	Marine
Rhynie Chert	Devonian	Aberdeenshire, Scotland	Terrestrial
Cleveland Shale	Devonian	Ohio, USA	Marine
Lesmahagow Inlier	Silurian	Lanarkshire, Scotland	Marine
Eurypterid Dolomite (Rootsikula Stage)	Silurian	Saaremaa, Estonia	Marine
Waukesha Dolomite (Brandon Bridge)	Silurian	Wisconsin, USA	Marine
Beecher's Trilobite Bed (Frankfort Shale)	Ordovician	New York, USA	Marine
Anthraconite (Orsten)	Cambrian	Sweden	Marine
Burgess Shale (Stephen Formation)	Cambrian	British Columbia	Marine
Spence Shale	Cambrian	Utah, USA	Marine
Wheeler Formation	Cambrian	Utah, USA	Marine
Emu Bay Shale	Cambrian	Kangaroo Island, Australia	Marine
Kinzers Formation	Cambrian	Pennsylvania, USA	Marine
Pound Quartzite	Vendian	Flinders Ranges, Australia	Marine
Valdai Series	Vendian	Onega Peninsula, USSR	Marine
Nama Group	Vendian	Namibia	Marine
Conception Group	Vendian (?late Riphean)	Avalon Peninsula, Newfoundland	Marine

post-Vendian rise of scavengers and predators (see above) and greater churning of the sediment, conditions for preservation of soft-bodied and lightly skeletized species with a generally minimal fossilization potential became more localized (Sepkoski 1979). Amongst the post-Ediacaran faunas the continuum in preservational quality that exists in sedimentary rocks means that there are no clear-cut criteria to determine whether a given fossil fauna or flora should be regarded as an exceptional Lagerstätte. For instance, there are many additional horizons, e.g. various 'insect beds' or 'fish beds', which could qualify for inclusion in Table 5. Even the Lagerstätten in Table 5 do not possess equal status. It is generally agreed that amongst the most significant are the Solnhofen Limestone, Mazon Creek (Francis Creek Shale) ironstone nodules, Hunsrückschiefer, and Burgess Shale. To what

extent their pre-eminence is due to greater diversity and related perfection of preservation, extent of collecting, ease of geographical access, and attendant scientific publicity is uncertain. The principal purpose of Table 5, however, is not to present an exhaustive compilation, but to emphasize the abundance of these Lagerstätten through geological time.

Are Lagerstätten representative?

Incorporating data from Lagerstätten into the mainstream of palaeoecological research, that otherwise relies almost wholly on hard-part remains, may have advantages but is not without its pitfalls. A more systematic approach to the study of Lagerstätten in the context of the continuum of surrounding biotas (Schram 1979; Conway Morris 1981) is overdue. Nevertheless, it would be naïve to imagine that these Lagerstätten can be used as a simple panacea in palaeoecological analysis. Soft-part preservation frequently entails anoxic or hypersaline conditions, thereby excluding scavengers and perhaps diminishing rates of microbial decay. The necessary proximity of a benthic biota, perhaps adapted to unusual environmental conditions, or even restriction of the biota to a pelagic element occupying the aerated top of a water column, means that the preserved assemblage cannot be representative in comparison with those inhabiting 'normal' environments. Moreover, a biota occupying areas where catastrophic burial is favoured need not necessarily be representative (see also Brett and Eckert 1982). Perusal of the literature on Lagerstätten makes the above discussion abundantly clear (see Whittington and Conway Morris 1985). There are repeated references to an absence or rarity of otherwise abundant groups, e.g. stenohaline brachiopods, trilobites, echinoderms, a limited benthic component with emphasis on pelagic elements (e.g. fish), or preservational bias towards organisms of small size (e.g. amber, Orsten), or limited escape abilities following catastrophic burial. On the other hand some Lagerstätten do appear to represent a more or less normal assemblage and, as was argued above, the likelihood that the Phyllopod Bed community falls into this category suggests that inferences based on its ecology may have a wider application.

Future research

A neglected role of Lagerstätten is their possible use in assessing diversity changes through the Phanerozoic (Cisne 1974). Concerning this, Raup (1972) considered that Lagerstätten would have a largely disruptive effect on calculations by adding 'noise' to the available data, and specific instances of this were documented by Hoffman and Ghiold (1985). Sepkoski (1981*b*) indicated that when considering the total of marine metazoan families through the Phanerozoic, information derived from Lagerstätten is of little significance. Nevertheless, about one fifth of the marine metazoan clades are known only from three major Palaeozoic Lagerstätten (Burgess Shale, Hunsrückschiefer, Mazon Creek) (Sepkoski 1981*b*).

The final area that deserves comment is the ignorance surrounding the diagenetic conditions leading to exceptional preservation. While the overall mode of preservation is evident (e.g. pyrite, siderite, carbonaceous residues, phosphates, silica or silicates), the ultrastructure of replacement is poorly known. Thus, Cisne (1981) commented on the erratic extent of pyritization in trilobites with appendages from Beecher's Trilobite Bed (Frankfort Shale), and the controlling factors are not well understood. The underlying physico-chemical conditions that led to special preservation are obscure, but it is likely that in some cases bacteria (e.g. Wuttke 1983*a*) may have had a significant intermediate role. The unusual conditions make laboratory replication difficult and pioneer studies by workers such as Hecht (1933), Zangerl and Richardson (1963), Oehler and Schopf (1971), Zangerl (1971), Leo and Barghoorn (1976), Francis *et al.* (1978), and Wuttke (1983*b*) need further development. Work in progress on the ultrastructure of soft-part preservation may provide new insights.

CONCLUSIONS

On the basis of a shelly assemblage little different from those that characterize many Cambrian faunas, the soft-bodied biota of the Phyllopod Bed (Burgess Shale) is regarded as reasonably representative, at least with regard to moderately deep-water communities living in the Cordilleran region. The shelly assemblage in the Phyllopod Bed accounts for no more than 20% of genera, and

perhaps as little as 2% (excluding sponges) in terms of individuals. Accordingly, the soft-bodied component is important in reconstructing the ecology of this community and, by implication, certain other Cambrian faunas. The analysis of the fauna is undertaken in terms of taxa (number of genera, mostly monospecific), individuals, and biovolumes. Ecological categories are defined according to position relative to substrate and degree of mobility, and feeding type. Of particular importance in the benthic assemblage are epifaunal vagrant deposit feeders (mostly arthropods), infaunal vagrant carnivores/scavengers (priapulid worms), epifaunal sessile suspension feeders (almost entirely sponges and brachiopods), and infaunal sessile suspension feeders (probable hemichordates). The Phyllopod Bed fauna shows unequivocally that the fundamental trophic structure of marine metazoan life was established early in its evolution (see Hutchinson 1959, 1961; Bretsky 1969). Highlights of the trophic analysis include: *a*, the identification of a trophic nucleus (text-fig. 10) dominated by relatively few taxa, although the composition varies according to whether the nucleus is considered in terms of either individuals or biovolumes; *b*, the recognition of the importance of carnivores and scavengers; and *c*, the reconstruction of a trophic web (text-fig. 11) and crude estimates of energetic efficiency between the levels of primary and secondary consumers. Possible niche structure of various ecological categories is addressed via dominance-diversity curves (text-fig. 12). Most show a log-normal distribution which may have no simple ecological explanation. However, examples of a geometric distribution, such as in epifaunal vagrant deposit (collector) feeders (EVDC), could be consistent with the hypothesis of niche pre-emption.

An attempt is made to trace ecological analogues of the Phyllopod Bed community in deeper-water assemblages through geological time (Cambrian-Devonian) with particular reference to the trophic categories of carnivores and scavengers, deposit feeders, and suspension feeders. Taxonomic membership of such a category may show continuity for a protracted period; for example, the apparent persistence of trilobites and ostracodes as deposit feeders. In other cases, however, innovation in the form of new groups either insinuating or perhaps replacing more archaic forms appears to have occurred. The appearance of carnivores and scavengers, such as nautiloids and eunicid polychaetes, may be an example. How far the evolution of such ecological units can be usefully traced through time is uncertain. If claims that the oxygen levels of Palaeozoic oceans were lower than today have any validity, then examination of dysaerobic faunas through geological time might provide insights into the evolution of ecological units. It must be admitted, however, that modern dysaerobic faunas (e.g. Savrda *et al.* 1984; Thompson *et al.* 1985) do not appear to have any striking ecological similarities with Palaeozoic assemblages.

The paper concludes by calling attention to the frequency of soft-bodied Lagerstätten (Table 5) and emphasizes their role as potential sources of palaeoecological information. The extent to which such exceptional biotas can be regarded as representative in comparison with coeval shelly assemblages requires examination, as do the physico-chemical conditions responsible for promoting such remarkable preservation in the geological record.

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APPENDIX

*List of institutions with holdings of Burgess Shale material**

Adelaide, Department of Geology and Geophysics (Australia)
Birmingham, Department of Geology (UK)
Bristol, Department of Geology (UK)
Cambridge, Museum of Comparative Zoology at Harvard (USA)
Cambridge, Sedgwick Museum (UK)
Cardiff, National Museum of Wales (UK)
Chicago, Field Museum (USA)
Cincinnati, Department of Geology (USA)
Cincinnati, Museum of Natural History (USA)
Colorado Springs, Department of Geology (USA)

* Information regarding additional listings will be welcomed by the author.

Lancaster, North Museum, Franklin and Marshall College (USA)
London, Department of Palaeontology, British Museum (Natural History) (UK)
London, Department of Geology, University College (UK)
Lund, Department of Geology (Sweden)
Melbourne, National Museum of Victoria (Australia)
Missoula, Department of Geology (USA)
Montreal, Redpath Museum (Canada)
New Haven, Peabody Museum (USA)
New York, American Museum of Natural History (USA)
Oslo, Paleontologisk Museum (Norway)
Ottawa, Geological Survey of Canada (Canada)
Perth, Department of Geology (Australia)
Pittsburgh, Carnegie Museum (USA)
Stuttgart, Staatliches Museum (Federal Republic of Germany)
Sydney, Department of Geology and Geophysics (Australia)
Toronto, Royal Ontario Museum (Canada)†
Tubingen, Institute and Museum of Geology and Palaeontology (Federal Republic of Germany)
Uppsala, Palaeontological Institute (Sweden)
Washington, DC, National Museum of Natural History (USA)

† Small collections distributed by R.O.M. to many institutions in Canada.